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Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs.

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Summary

The effects of plants on the biosphere, atmosphere, and geosphere are key determinants of terrestrial ecosystem functioning. However, despite substantial progress made regarding plant belowground components, we are still only beginning to explore the complex relationships between root traits and functions. Drawing on literature in plant physiology, ecophysiology, ecology, agronomy and soil science, we review 24 aspects of plant and ecosystem functioning and their relationships with a number of traits of root systems, including aspects of architecture, physiology, morphology, anatomy, chemistry, biomechanics and biotic interactions. Based on this assessment, we critically evaluate the current strengths and gaps in our knowledge, and identify future research challenges in the field of root ecology. Most importantly, we found that below-ground traits with widest importance in plant and ecosystem

functioning are not those most commonly measured. Also, the fair estimation of trait relative importance for functioning requires us to consider a more comprehensive range of functionally-relevant traits from a diverse range of species, across environments and over time series. We also advocate that establishing causal hierarchical links among root traits will provide a hypothesis-based framework to identify the most parsimonious sets of traits with strongest influence on the functions, and to link genotypes to plant and ecosystem functioning.

Keywords: below-ground ecology; ecosystem properties and processes; environmental gradients; plant functions; root traits; spatial and temporal scales; trait covariation; trait causal relationships

I. Introduction

Plants are powerful ecosystem engineers. Extending both above- and below-ground, sometimes to a great height and depth, they shape the biosphere and its interactions with the uppermost lithosphere, the hydrosphere and the atmosphere (de Kroon & Visser, 2003; Schenk & Jackson, 2005). Taken together, the effects of plants on the biosphere, atmosphere, and geosphere are key determinants of terrestrial ecosystem functioning. Below-ground, plant roots and their symbionts are central to the maintenance of multiple ecosystem functions (Bardgett *et al.*, 2014; Freschet & Roumet, 2017): roots play key roles in the transformation and circulation of elements and mineral/organic compounds across the spheres (Prieto *et al.*, 2012; Freschet *et al.*, 2018b), and particularly in the formation, maintenance and stabilisation of soils (Daynes *et al.*, 2013; Dignac *et al.*, 2017). Thus, an advanced mechanistic understanding of the effects of root systems on ecosystem functions has numerous potential applications, such as designing plant mixtures for nutrient retention in agrosystems, for stabilization of hillslopes, etc. (Stokes *et al.*, 2009; Lavorel *et al.*, 2013; Martin & Isaac, 2015).

Root systems, among other plant parts, show a tremendous diversity of forms and properties (Kutschera, 1960; Robinson *et al.*, 2003; Bodner *et al.*, 2013; Iversen *et al.*, 2017). In recent decades, parallel developments in many areas of root research (e.g. morphology, physiology, architecture, biomechanics and anatomy, among others) have brought considerable advances in our understanding of the diversity in root traits and their

contribution to plant and ecosystem functioning (Freschet *et al.*, 2020). Such advances are key to strengthening the foundations of current dominating theoretical frameworks, often built on data from the same few easily-measurable traits (McGill *et al.*, 2006; Reich *et al.*, 2014). For example, recent attempts to assemble a diverse set of trait data from a range of disciplines in root science permitted researchers to move from a single root economics spectrum (Reich *et al.*, 2014; Roumet *et al.*, 2016) that only poorly explained root trait variation and its impact on plant performance (Weemstra *et al.*, 2016), towards a multidimensional 'root economics space' that further integrates aspects of symbiotic associations and is supported by traits closely related to functioning (Bergmann *et al.*, 2020). However, despite major progress, numerous gaps remain in our understanding of trait-functioning relationships and we still lack a comprehensive overview of available knowledge that bridges research fields.

Here, sharing expertise from a range of fields in root research, we first synthesise recent advances in our understanding of demonstrated relationships between root traits and plant or ecosystem functioning (section-II, see Tables 1 & 2 and Fig. 1 for an overview of this broad assessment). Additionally, two examples are more comprehensively assessed in order to illustrate the multiple direct and indirect roles of root traits as drivers of i) plant functioning, with an investigation of the relationships between root traits and plant nitrogen (N) uptake capacity, and ii) ecosystem functioning, by examining the linkages between root traits and soil reinforcement against shallow landslides (see Tables 3 & 4 and Fig. 2 for an overview of these comprehensive assessments). Based on this two-step assessment, we critically evaluate the current strengths and gaps in our knowledge, and identify research challenges for the future. Specifically, we address three main research avenues that offer potential to improve our understanding of trait-function relationships. First, we consider the importance of using an informed selection of traits for exploring root trait-functioning relationships and discuss how sets of currently understudied traits may provide more insights than common, easy-to-measure traits (section-III). We then discuss how our understanding of trait-trait relationships and hierarchies among traits can help us to advance our knowledge of the synergistic or antagonistic effects of different traits on plant and ecosystem functioning, and lead us one step further in linking genotypes to function (section-IV). Next, we address the opportunities and pitfalls when generalising trait-functioning patterns across plant species, growth forms, environmental contexts, and temporal and spatial scales (section-V). Our two examples of plant and ecosystem functioning are woven through the remainder of this paper to illustrate our purpose.

II. An overview of trait-functioning relationships: rationale and limitations

To explore relationships between root traits and functions, we performed a broad, multidisciplinary assessment of empirical and demonstrated links between below-ground traits and plant and ecosystem functioning (Tables 1 & 2). To do so, we first identified 15 key plant functions (Table 1) and nine ecosystem processes and properties (Table 2) based on their relevance to the functioning of natural and managed ecosystems. Drawing on literature in the fields of plant physiology, ecophysiology, ecology and soil science, we considered reviews and empirical studies where both root traits and functions were measured or conceptualised. We considered traits relevant for 16 research fields (as distinguished in Freschet *et al.*, 2020; Fig. 1d), taking in aspects of root system architecture, physiology, morphology, anatomy, chemistry, biomechanics and biotic interactions. For each function we report: i) the root trait measured and its relationship to a function (positive or negative); ii) below-ground plant entities (e.g. root type, see Freschet *et al.*, 2020) on which the trait would be most relevant to measure; and iii) contextual information explaining the rationale for and degree of confidence in the relationship (Tables 1 & 2).

Trait selection was motivated by both the presence of a defined mechanistic relationship and empirical observations under controlled conditions or *in situ*. However, Tables 1 & 2 are not consolidated accounts of demonstrated evidence. Most studies reported here cover only a handful of species; as such, they may rely on fortuitous relationships resulting from interactions among traits (as discussed in section-III) and on context-dependent observations that may not be widely generalizable across multiple species and biomes (see section-IV). In addition, we stress that Tables 1 & 2 represent neither an exhaustive list of important traits nor all relevant references, but rather a broad overview of current knowledge where most relationships await confirmation. Highlighted key studies are provided to guide the audience to further reading.

Due to the limited, often contradictory state of current knowledge of root trait-functioning relationships, we do not attempt to estimate the importance of the relationship but merely indicate current evidence for its existence (i.e. a single trait impacts a specific function). Our understanding of results from past studies is particularly limited by a range of methodological issues. This includes the absence of purposeful selection of complementary traits and root entities (see section-III), the lack of accounting for trait covariation and hierarchy (see section-IV), or the lack of knowledge on the influence of genetic diversity, environmental variation and scaling across temporal and spatial scales (see section-V).

Despite these limitations, Tables 1 & 2 are useful because they provide an indication of the range of empirical and theoretical relationships between below-ground traits and plant and ecosystem functioning across research fields; link these relationships to selected references and standardized trait measurement protocols (as described in the handbook of root traits, see Freschet *et al.*, 2020); and highlight a number of rarely considered traits in order to connect different fields.

III. Trait selection

1. Measuring a complementary range of traits: are we focusing on the right ones?

Recent decades have seen the rise of approaches using a few easily measurable traits to capture plant and ecosystem functioning. Given the difficulties associated with specialized measurements of some key physiological, anatomical or chemical traits, most local-scale studies, which later feed global-scale analyses, make use of 'soft' traits (i.e. easily measurable traits, often vaguely related to a single or a number of functions) only, rather than a range of soft and 'hard' traits (i.e. those difficult to measure, but often more closely related to a precise function) selected on the basis of a comprehensive review of potentially relevant mechanisms or processes (but see for instance Maire *et al.*, 2009; Belluau & Shipley, 2018; Freschet *et al.*, 2018a; Ros *et al.*, 2018). For example, at the time of this survey, the FRED database (the most extensive fine-root trait database to date; Iversen *et al.*, 2017) comprises a large number of observations for the five traits most easily measured (~5000 entries for root N concentration and classical morphological traits such as root diameter and specific root length, ~3200 for root tissue density), whereas only ~320 entries for indicators of root N uptake (e.g. net ion uptake rate, maximum net ion uptake rate) and ~220 observations for indicators of root exudation (e.g. acid phosphatase activity, carbon exudation rate). Here, we stress that if a trait is widely measured, it does not necessarily mean that it is of key functional importance. During the construction of Tables 1 & 2, many trait-functioning relationships appeared indirect, vaguely justified and/or poorly tested and led us to question the broad relevance of those traits most commonly measured for plant and ecosystem functioning. Moreover, Tables 1 & 2 and Fig. 1 underscore that most ecosystem functions are likely influenced by a wider range of traits than typically assumed (McCormack *et al.*, 2017; Freschet *et al.*, 2020). In this respect, our review strengthens the idea that the search for simplified and generalizable patterns should not be at the expense of the mechanistic understanding of trait-functioning

relationships (Shipley *et al.*, 2016; Belluau & Shipley, 2018). As such, we hope that Tables 1 & 2 will stimulate a debate on the merits of the classical notion that we must, by necessity, choose between studying few traits with a clear 'functional importance' or many easily measured traits (Belluau & Shipley, 2018; Freschet *et al.*, 2018a).

Root N concentration, one of the most frequently measured root traits, provides a good illustration of the common discrepancy between the frequency of trait measurements and their functional importance. Clearly important for ecosystem N cycling, root N is often measured for its presumed role in determining the overall metabolic activity (Reich *et al.*, 2008; Roumet *et al.*, 2016) and, by extension, may be assumed to scale up proportionally with specific root uptake activities (e.g. Grassein *et al.*, 2018). For example, above-ground we know that leaf N concentration is indeed strongly linked to leaf photosynthetic capacity, with more than 60% of leaf N contained in leaf photosynthetic compartments (Evans & Seemann, 1989). However, although root N concentration is a good predictor of specific root respiration (Reich *et al.*, 2008, 67 species, R^2 = 0.69; Roumet *et al.*, 2016, 73 species, R^2 = 0.25) (Fig. 2), the multiple functional roles of root N (including nutrient uptake and assimilation, but also transport, defence compounds and stored N) imply that its use as an indicator of specific activities may remain highly speculative (Table 1, Fig. 2a).

Specific root length (SRL) serves as another example of a very commonly measured but little understood 'soft' trait. It is typically interpreted as a large root surface (i.e. equivalent to specific root area) at a low cost of root construction, and is therefore assumed to mirror specific leaf area (Reich, 2014) and act as a gauge for soil resource uptake efficiency (Ostonen *et al.*, 2007). However, while this description is true, it is strongly reductive. First, it is not so much the surface of roots that would matter for below-ground resource uptake, but rather the volume of soil under influence by the root (e.g. the nitrate depletion zone around the root, or the frequency of root encounters during the flow of solutes in the soil), which depends more strongly on the length of roots deployed rather than its surface. Specific root length may thus be better referred to as a proxy for the volume of soil under influence by the root, and will most often be more closely related to soil resource uptake efficiency than specific root area. Second, it is rarely considered that cheaply constructed roots may have a much shorter lifespan (Ryser, 1996), and therefore, as a system, may have limited ability for long-term resource uptake, unless this trait is combined with a high root turnover rate. Third, SRL is a composite trait determined by the variation in root diameter and root tissue density (Fig. 2) and hence under control of complex internal plant construction trade-offs (Kong *et al.*, 2014; Poorter & Ryser, 2015). Fourth, it remains poorly understood to what extent SRL

trades-off with root mass fraction (Freschet *et al.*, 2015a; Weemstra *et al.*, 2020, Fig. 2) and mycorrhizal colonization (McCormack & Iversen, 2019; Bergmann *et al.*, 2020), and acts in synergy with root hairs (Forde & Lorenzo, 2001) and root branching density (Eissenstat *et al.*, 2015) to change the volume of soil explored or exploited by roots (*sensu* Lambers *et al.*, 2008; Freschet & Roumet, 2017). A close inspection of these aspects is needed to resolve why SRL has been sometimes found to positively correlate with N uptake rates across species (Reich *et al.*, 1998; Larson & Funk, 2016; Grassein *et al.*, 2018; Hong *et al.*, 2018, 30 species), but not in other cases (Grassein *et al.*, 2015; Bowsher *et al.*, 2016; Ravenek *et al.*, 2016; Freschet *et al.*, 2018a; Ma *et al.*, 2018, 48 species).

Root N concentration and SRL are just two examples of traits where a more correct, mechanistic framing is key to truly understanding the link between traits and plant and ecosystem functioning. This issue may be inherent to below-ground plant ecology, where the relevance of many 'soft' traits was presumed based on the mechanistic understanding of their above-ground counterparts, but with little scrutiny of their actual functional significance below-ground. Ultimately, the identification of key traits for plant and ecosystem functioning needs to come from larger sets of measurements in future studies that include both 'soft' and 'hard' traits.

2. Estimating the relative importance of traits

Furthering our mechanistic knowledge of trait-functioning relationships requires not only the identification of traits that are relevant for a function (see Tables 1 & 2), but also a consideration of the relative importance of these traits for the function. The relative importance of traits identified in Tables 1 & 2 is sometimes not known and often assumed, but rarely tested. To complicate the picture further, there is ample evidence from case studies that environmental conditions interact to shuffle the relative importance of traits for individual functions, possibly due to variations in costs and benefits of a given plant strategy. For example, the relative importance of a plant's ability to fix N_2 in symbiosis with microbes strongly increases as soil N availability decreases, while in turn N_2 fixation becomes increasingly constrained as soil P availability decreases (Batterman *et al.*, 2013b). In a second example at the ecosystem level, efficient root hydraulic conductance can rapidly dry wet soil in climates with discontinuous rain events (e.g. Boldrin *et al.*, 2017), and therefore help protect against shallow landslides. However, in climates with prolonged rainy seasons and

with soils that are close to saturation for long periods of time, the efficiency of this trait is lost and the mechanical traits become more efficient at reinforcing soil (Kim *et al.*, 2017). Also, there can be distinct thresholds in the ability of traits to serve functions. For example, along a gradient of soil P availability, the dominant plant species strategy tend to shift from the reliance on thin roots at high P levels, towards increasing reliance on high root hair density and mycorrhizal symbiosis at low P levels, and eventually towards the use of highly specialized structures such as cluster roots on severely P-impoverished soils (Lambers *et al.*, 2008).

In summary, few studies to date have quantified comprehensive sets of relevant root traits across a range of species with contrasting ability to perform a function, or replicated such setups along environmental gradients (but see first attempts by Belluau & Shipley, 2018; Freschet *et al.*, 2018a; Ros *et al.*, 2018; Henneron *et al.*, 2020). Moreover, most studies do not measure the actual function of interest, but more easily measurable proxies for the function (e.g. 'long-term N accumulation in plants' rather than 'long-term uptake rate'; 'centrifuge model estimate' instead of 'in-situ measurement' of soil shear reinforcement; see Tables 3 & 4). Although measuring the actual function often proves challenging, additional efforts may be needed to improve the relatedness of our proxies to the functions.

3. Considering multiple root types

To fully appreciate and understand the impact of root traits on plant or ecosystem functioning, consideration of what portion of the root system and root types are involved is needed (McCormack *et al.*, 2015a; Klimešová *et al.*, 2018). Different parts of a root system may be important for distinct aspects of plant and soil functioning (Freschet & Roumet, 2017). For example, when studying the contribution of vegetation to soil reinforcement against shallow landslides, studying the entire root system is key to capturing the distribution of root diameters that cross the multiple potential shear (rupture) surfaces along a slope (Stokes *et al.*, 2009). Thick structural roots act like soil nails, preventing soil collapse due to their mass, bending strength and stiffness. Thin and fine roots anchor plants to deeper soil layers (beneath the shear surface) and need to be strong when held under tension. Although several geotechnical models have considered the contribution of roots, irrespective of root types, to the reinforcement of potential shear planes that lie parallel to the soil surface (Table 4), these models generally overestimate slope stability, highlighting the need to better differentiate between the effects of distinct root types (Schwarz *et al.*, 2010; Mao *et al.*, 2014).

With respect to N uptake by wheat (*Triticum aestivum*), average rates of uptake per unit length of root may be only a small proportion of predicted uptake rates (Robinson *et al.*, 1991), probably due to a combination of physiological differences between individual roots and spatial clustering of root distribution. Using ion-selective microelectrode techniques, the most rapid N uptake was indeed found between 0 and 40 mm behind the root tip, decreasing between 40 and 60 mm (Plassard *et al.*, 2002; Miller & Cramer, 2004). However, this longitudinal decrease may represent only a 2- to 3-fold difference in uptake rate, with transporter gene expression studies suggesting that mature parts of the root remain significant sites of uptake (Miller & Cramer, 2004; Hawkins *et al.*, 2014). In maize (*Zea mays*), a non-destructive method was developed to fit small chambers around short root segments in hydroponics in order to measure starting and ending nitrate concentration to calculate net influx, which allowed simultaneous measurements of several root types and positions along the roots. By comparing 15-day and 20-day old plants, this study showed that maximum uptake rate may increase as the plant N demand increases, and that variation for this rate exists among lateral roots, basal roots, and shoot-borne roots (York *et al.*, 2016). Overall, despite growing knowledge on how root anatomy differs across root orders, much remains uncertain about how N uptake varies, and how this might differ among herbaceous and woody species (e.g. Hawkins *et al.*, 2014) and across environments (Gessler *et al.*, 2005).

These examples illustrate that much effort is required to further our knowledge of how various plant parts relate to specific functions. The spatial distribution of specific type of roots in the soil, and their ability to perform their function, is clearly dependent on the attributes of the rest of the root system. Focusing on trait-functioning relationships of a single root type may provide an incomplete picture of plant functioning and effects on ecosystem functions.

4. Towards widespread consideration of other types of traits

Our overview of root trait-functioning relationships (Tables 1 & 2), and the visual illustration of their interconnections (Fig. 1), suggests that many understudied traits may be crucial for a range of plant functions and ecosystem properties and processes. Three categories of traits are frequently highlighted (Fig. 1d): those associated with mycorrhizal associations, belowground allocation and the spatial distribution of roots. More specifically, among other traits, mycorrhizal association type and colonization intensity, root length density and root mass fraction, root branching density, root hair length and density, vertical root distribution index

and maximum rooting depth are particularly represented in our synthesis of trait-functioning relationships (Fig. 1a-c). Described below, these traits can impact plant and ecosystem functioning in several ways:

i) The reliance of plants on different 'types of mycorrhizal fungi' (e.g. Read & Perez-Moreno, 2003; Phillips *et al.*, 2013) and the 'intensity of root colonization' serve as excellent indicators of the degree to which a plant makes the trade-off between relying on its own functional capability or on symbioses with fungal partners (Kong *et al.*, 2019; McCormack & Iversen, 2019; Bergmann *et al.*, 2020). Such critical determinants of plant resource acquisition and conservation strategies are also increasingly recognized as key drivers of a range of ecosystem properties and processes (Soudzilovskaia *et al.*, 2019).

ii) 'Root mass fraction' (or fine-root mass fraction, rhizome mass fraction, etc.) depicts the relative investment of biomass to specific belowground parts and therefore is a key trait in determining plant performance (Wilson, 1988; Poorter *et al.*, 2012). In association with SRL and total plant biomass, fine-root mass fraction determines total plant investment in fine-root length, which is a key determinant of the potential biophysical interactions between plants and the soil matrix.

iii) 'Root branching density' is increasingly recognized as a key determinant of root system architecture, with high branching density being typical of more clustered root systems favouring soil particle enmeshment and localised soil resource mining, and pre-emption against competitors (Forde & Lorenzo, 2001; Hodge, 2004). Low branching density, on the other hand, favours soil exploration (Eissenstat *et al.*, 2015) and may thus be most effective for the uptake of very mobile soil resources such as nitrate and water (e.g. Pedersen *et al.*, 2010).

iv) Maintaining high 'root hair length and density' is a very efficient way for plants to maintain root contact with soil particles (Carminati *et al.*, 2017), facilitate root anchorage and penetration into dense soils (Haling *et al.*, 2013; Choi & Cho, 2019), as well as reinforcing root interactions with the soil matrix (e.g. for resource uptake, exudation, connection to N_2-fixing symbionts, Holz *et al.*, 2018).

v) 'Vertical root distribution index' and 'maximum rooting depth' are additional descriptors of plant strategies to occupy soil volume and explore different horizons of soil (Freschet *et al.*, 2020). The localization of roots in soil has straightforward implications for the interactions between plants and soil and the transfer of elements, impacting plant resource acquisition and the recycling or sequestration of organic compounds along the soil profile (Jobbágy & Jackson, 2000; Poirier *et al.*, 2018; Mackay *et al.*, 2019).

While this set of traits merits further attention, the primary purpose of drawing up this subjective and non-exhaustive list is to emphasize that many dimensions of root effects on plant and ecosystem functioning require further consideration. Several 'hard' traits important for a range of functions (including some of the above-mentioned traits) present methodological challenges that limit their use (e.g. their study is labour-intensive, is not feasible in the field, requires complex equipment or implies known measurement inaccuracies). These challenges hinder conceptual formalization and testing of trait-functioning relationships, particularly in connection to other traits. Some of these important, but particularly challenging traits include physiological traits such as i) root exudation rate, ii) root exudate composition, iii) root respiration, iv) root enzymatic activities, v) root nutrient absorption (and the synergistic role of mycorrhizal fungi) and vi) root nutrient resorption processes, which are important determinants of nutrient uptake and cycling, chemical and anatomical aspects of vii) root resistance to pathogens and viii) root resistance to mechanical stresses, and aspects of ix) root persistence and turnover in soils that further impact soil nutrient and ecosystem carbon cycling. While an exhaustive review of recent advances in the measurement of these 'hard' traits is beyond the scope of this synthesis, we emphasize that a range of studies are already bringing improvements that facilitate such challenging measurements (see for instance Phillips *et al.*, 2008 for soluble root exudates; Lak *et al.*, 2020, for specific root respiration; Griffiths *et al.*, 2020, for multiple ion-uptake phenotyping; Arnaud *et al.*, 2019, for in-situ root imaging)

IV. Trait-trait relationships

1. Considering trait inter-relations

The individual effects of root traits on plant and ecosystem functioning are not easy to single out (Lavorel & Garnier, 2002; Lavorel *et al.*, 2013) (Fig. 1, 2). The range of trade-offs and synergies typically observed among traits (Poorter *et al.*, 2013; Roumet *et al.*, 2016; Weemstra *et al.*, 2016) suggests that plant internal (construction or evolutionary) constraints are likely to limit the number of possible adaptations of plants to environmental conditions. Figure 2 provides a range of examples where causal relationships between traits during tissue construction leads to trade-offs (e.g. mycorrhizal colonization intensity typically covaries negatively with SRL owing to the opposite effects of root cortex area fraction on the two

traits) or synergies (e.g. root bending resistance and root elastic modulus typically covary positively owing to the strong positive influence of lignin and cellulose concentrations on these two traits). The result of these constraints can be seen at both the intra-species and inter-species level. Therefore, a change in the expression of one trait may have several direct consequences for the expression of other traits. This network of inter-relations, as depicted in Fig. 2a and b by causal relationships and trait covariation connectors, is often very complex.

In addition, any trait that helps alleviate a limitation or adapt to a stress, changes the strength of the limitation/stress signal, which may reduce the need for other trait adjustments (Freschet *et al.*, 2018a). As an example of this, Freschet *et al.* (2015a) showed that in a given environment most plant species tend to achieve similar levels of root length per mass of plant by developing either high SRL or high root mass fraction (depicted as causal links in Fig. 2a). This observation holds across several levels of soil N availability (Freschet *et al.*, 2015b). In this context, it appears reasonable to assume that under non-extreme resource limitation or stress conditions, different combinations of root trait values (e.g. high SRL and root hair length and density *versus* high root mass fraction and mycorrhizal colonization intensity) may result in a similar outcome with regard to plant function (e.g. N uptake capacity) (Marks & Lechowicz, 2006; Weemstra *et al.*, 2020).

The variability of plant growth strategies also implies a range of interactions between root traits, with non-additive effects on plant and ecosystem functioning. For example, a species with a deep root system, high reliance on mycorrhiza and low litter decomposability may have a strong positive effect on soil organic carbon stock via deep soil carbon sequestration, whereas a similar species with shallow rooting may have only a marginal effect on soil carbon (e.g. Clemmensen *et al.*, 2013). Similarly, although a deep rooting species may improve resistance to landslides and water uptake at depth, its effect will be noticeable only if a substantial amount of roots is found at depth (e.g. if it has a high index of vertical root distribution) (Stokes *et al.*, 2009).

Overall, it remains largely unknown whether syndromes of traits (i.e. consistent patterns of trait combinations; Bergmann *et al.*, 2020) or syndromes of plastic trait adjustments (i.e. consistent patterns of plastic changes; Freschet *et al.*, 2018) occur along well-characterized resource limitation, stress or disturbance gradients, or whether observed trends are mostly context-dependent (e.g. species-specific, community-specific). The identification of such syndromes may eventually help us summarize the covariation of trait values and their (antagonistic, additive, or synergistic) effects on plant and ecosystem function (Lavorel & Grigulis, 2012; Herben *et al.*, 2018). It would also help us discriminate between mechanistic

and fortuitous trait-functioning relationships. Much remains to be done to evaluate the existence and consistency of such inter-relations. First, only a few causal relationships and indirect covariations (as depicted by black and orange connectors, respectively, in Fig. 2) between root traits have been identified (and even less so across traits from the entire plant). Second, our knowledge is biased towards the aforementioned set of widely studied root traits (Fig. 2). Third, in complex natural environments, plants are subjected to many co-occurring environmental factors whose interaction is likely to drive trait expression in multiple directions simultaneously (e.g. Kumordzi *et al.*, 2019; Zhou *et al.*, 2019). This may limit the value of our knowledge of syndromes of traits and plastic trait adjustments recorded across single environmental gradients. Indeed, these trait and environment integrations significantly influence function and fitness landscapes in multidimensional space (York *et al.*, 2013), but more data are required to fully appreciate the complex relationships that are in place.

2. Accounting for causal relationships among traits

The functional or categorical grouping of individual root traits as illustrated by the horizontal dimension of Fig. 2 is useful to enhancing our understanding of plant and ecosystem function (McCormack *et al.*, 2017). At the same time, it is important to consider the causal relationships (or hierarchy) among traits, as represented by the vertical dimension of the same Figure (Fig. 2: vertical dimension, Rogers & Benfey, 2015). Many traits, referred to as composite traits, can be broken down into component (i.e. underlying) traits. For example, SRL emerges from the interaction between root diameter and root tissue density, which are themselves influenced by root cortex thickness and stele diameter (Fig. 2a). Root tissue density is further determined by the cortex and stele anatomical and chemical traits (Kong *et al.*, 2019). Composite traits are particularly used because they are seen as concise indicators of plant functioning and often have the most direct influence (i.e. mechanistic link) on ecosystem functioning (see Fig. 2). The drawback is that composite traits are under the influence of several component traits that do not necessarily vary in synchrony (e.g. Poorter & Ryser, 2015), and adjustments to even simple environmental gradients may therefore often be unpredictable. Specific root length is one key example of a trait that may be important for N uptake, but whose response to changes in N availability is highly variable (e.g. Poorter & Ryser, 2015; Freschet *et al.*, 2018a), owing to contrasting responses of its component traits to N availability.

An understanding of causal links (or more generally, hierarchical organisation) between root traits is useful for the following three purposes. First, it provides a mechanistic basis (i.e. the hypothesis-based framework) to interpret the outcome of statistical model selection procedures (i.e. the set of variables retained in multivariate models linking traits to functions) or structural equation models. As such, an understanding of trait hierarchical organisation will hold the key to the identification of the most parsimonious sets of traits with strongest influence on the functions. As an example, for defining root N uptake capacity, root diameter is mostly important due to its effect on SRL and its covariation with cortex area fraction (Fig. 2). Second, knowledge of hierarchical relationships aids the identification of component traits whose influence spans several composite traits. With respect to plant N uptake capacity, cortex thickness is one such trait. It was shown to enhance the potential for roots to host mycorrhizal fungi, which is beneficial for root-fungi associations (Kong *et al.*, 2017; Kong *et al.*, 2019). Cortex thickness also influences root diameter and root tissue density, which together determine SRL (Fig. 2). Therefore, despite being rarely measured, root cortex thickness underlies two of the most widely studied and measured morphological root traits and is of critical importance for the capacity to develop mycorrhizal symbiosis. Third, another key aspect of identifying component traits is the likelihood of being directly linked to plant genes. A better understanding of the component traits' genetics—and its regulation under given environmental conditions—will not only provide an evolutionary explanation of key (composite) traits and their selection, but may also foster breeding for root traits beneficial to a specific plant function. In this context, it would be useful to further differentiate between "genuine" composite traits, that are composed by traits with different (sets of) quantitative-trait loci (QTLs) responsible for each different component trait, from "integrated" composite traits where the underlying component traits are varying in a coordinated way as determined by pleiotropic, highly-linked QTLs or tight hormonal control—with nuances between those two extremes.

V. Generalizing across scales

1. Generalizing across species, plant growth forms and biomes

Our review of conceptual, experimental and observational studies of 24 aspects of plant and ecosystem functioning (Tables 1 & 2), and two detailed examples (Fig. 2a,b; Tables 3 & 4), emphasizes that the current knowledge of trait-functioning relationships relies on highly

variable numbers of observations covering the range of traits and functions. The majority of these relationships are based on relatively few species from a narrow range of plant growth forms and most have not been replicated along environmental gradients or across contrasting climates and soil types. Some trait-functioning relationships have been established in the field, while others come from pot monoculture or common-garden experiments. In this context, generalising these relationships is hazardous. As discussed above, different sets of species or growth forms may display different syndromes of traits, which further vary along gradients, and may therefore display different trait-function relationships. With respect to direct measurements of soil reinforcement to protect against landslides, only two studies could be found that consider more than three species, and virtually all studies consider only one growth form in one location (Table 4). Regarding N uptake capacity, most studies target herbaceous species at the same growth stage and often grown in hydroponics or pot conditions (Table 3), which questions whether knowledge gained from these highly simplified systems can be generalized to natural systems.

Overall, large differences have been observed across contrasting environmental contexts, such as across biomes. With regard to plant N uptake, we know for example that the importance of N-fixation strongly decreases from early successional to late successional forests of the temperate biome, whereas its importance remains high along similar gradients in the tropics (Batterman *et al.*, 2013a). Mycorrhizal effects on N uptake also vary strongly across biomes, with ectomycorrhizal fungi transferring less N to their hosts in biomes at higher latitudes than in tropical forests (Mayor *et al.*, 2015). Such examples illustrate that results gained in one system are unlikely to be directly generalizable to other systems.

Generally, further research bridging species from different plant growth forms and growing in contrasting environmental contexts is strongly needed to better inform our knowledge of trait-function relationships.

2. Meeting the challenge of up-scaling

Understanding the linkages between functional traits and plant and ecosystem functioning is often most critical at large spatial scales (e.g. entire agroecosystems or natural ecosystems, Suding *et al.*, 2008; Martin & Isaac, 2015). Several functional trait-based up-scaling approaches have been proposed to link plant traits to ecosystem functioning, including the community-weighted-mean trait approach (Lavorel & Garnier, 2002; Violle *et al.*, 2007) and

the pooled-species approach (Klumpp & Soussana, 2009; Prieto *et al.*, 2016). In the former, species are individually sampled (or non-destructively analysed), plant traits are measured at the level of individual species and a community trait value is calculated by weighting the trait values measured by the proportion that each species represents in the community (e.g., in terms of biomass or ground area cover). In the latter, pools of plants are sampled (or non-destructively analysed) over given ground area or soil volume and a community trait value is directly measured. In both instances, appropriate sampling resolution is key to capture a mix of plant organs representative of the community (see for example Ottaviani *et al.*, 2020), as biotic and abiotic variations occur at multiple spatial scales, (e.g. changing spatial trophic networks, soil properties, Tscharntke *et al.*, 2005).

Whether in the community-weighted-mean trait approach or pooled-species trait approach, effects on ecosystem functioning are typically assumed to be proportional to abundance (which can be expressed per unit root biomass, length or surface) to determine the functioning of the whole system (Grime, 1998; Garnier *et al.*, 2004). However, there are multiple reasons why such an approach can only capture parts of the plant community and ecosystem functioning. Depending on the system: (i) diversity effects, including competition, complementarity and facilitation, can add to the effect of species taken individually (e.g. Hodge, 2003; Santonja *et al.*, 2017; Mahaut *et al.*, 2019); (ii) some subordinate species can produce disproportionate effects on ecosystem functioning (Mariotte, 2014); (iii) interactions across multiple trophic levels can drive plant community and ecosystem function (Lavorel *et al.*, 2013); (iv) the relative importance of traits shifts depending on the environmental context (e.g. Lambers *et al.*, 2008); (v) small to large scale heterogeneity in ecosystem composition and function can maintain substantial levels of ecosystem function across all scales (Tscharntke *et al.*, 2005); and (vi) feedbacks between biotic and abiotic components, critical for ecosystem functioning and stability (Veldhuis *et al.*, 2018), are not apparent by considering the biotic components alone. For these reasons, scaling up from species traits or pooled-species traits to ecosystem-level functioning must be done with caution, and especially so in natural and semi-natural systems where biotic and abiotic interactions are even more complex than in low-diversity agricultural fields.

Nonetheless, the endeavour of up-scaling from traits to community and ecosystem yields multiple benefits. Most importantly, it provides a mechanistic framework (using or generating causal hypotheses for observed relationships) to test the contributions of traits (from species or pooled-species) to community and ecosystem functioning (Lavorel & Grigulis, 2012). Up-scaling also has the potential to fill in the gap between the small-scale

mechanistic understanding of reduced systems and large-scale integrative, but mostly descriptive assessments. In that respect, the community-weighted-mean trait and pooled-species trait approaches represent complementary approaches to tackle the problem at different levels of reductionism. Both approaches have advantages and drawbacks. Clearly, the pooled-species approach is far less time consuming when studying roots and limits the biases associated with estimations of root abundance (Ottaviani *et al.*, 2020) and root species identification. As such, this approach would generally help integrating aspects of both spatial and temporal variation in community trait – ecosystem functioning relationships (as discussed below), especially in ecosystems with large numbers of dominant and subordinate species. However, with respect to ecological modelling, since plant community composition varies across geographical location and time, such measurements of community traits are unlikely to be reused to predict ecosystem functioning from the crossing of community traits with species composition databases; as such, species-level traits might be preferred.

So far, few studies have tested to what extent the knowledge gained on the linkages between single species or pooled-species functional traits and plant and ecosystem functioning can be used to infer such relationships in complex ecosystems (Garnier *et al.*, 2004; Vile *et al.*, 2006; Hales, 2018; De Long *et al.*, 2019). Taking the example of root trait effects on plant N uptake, empirical studies most often measure the physiological ability of distinct species to take up N under controlled conditions (hydroponics or pot experiments, e.g. Maire *et al.*, 2009; Grassein *et al.*, 2015), or quantify community-wide N uptake based on the budgeting approach (e.g. Finzi *et al.*, 2007), ^{15}N labelling (Hong *et al.*, 2018) or even molecular approaches quantifying gene expression (e.g. Kraiser *et al.*, 2011). However, between these two extremes, few studies have attempted to explicitly relate ecosystem-scale measurements to individual species trait values (but see Gessler *et al.*, 1998; Craine *et al.*, 2002; Soussana *et al.*, 2005, 2012 for attempts with planted grass and tree species).

Interestingly, the reverse approach of down-scaling has sometimes been used successfully, starting from the observation of major differences in functioning between systems, and tracking back the causes to individual root traits. As an example, ectomycorrhizal *versus* arbuscular mycorrhizal dominated forests give rise to differences in coupled carbon-nitrogen cycling (see Phillips *et al.*, 2013; Wurzburger & Brookshire, 2017; Zhu *et al.*, 2018). Nonetheless, a species-level approach of root trait-soil function relationships would be useful to further identify the set of mechanistic linkages involved (Wurzburger & Clemmensen, 2018).

Another major challenge of up-scaling lies in the adequate characterization of plant community or ecosystem functioning at large scales. For example, soil reinforcement by roots at small scales (e.g. soil cores) is often used to predict resistance to landslides at the hillslope-scale, using geotechnical slope-scale models (e.g. Genet *et al.*, 2010), but validation of models in the field is usually limited. Although it is possible to perform controlled, slope-scale experimental tests (e.g. Schwarz *et al.*, 2010), and to physically model scaled-slopes in the laboratory (that reproduce the stress-distribution obtained in large-scale slopes, Sonnenberg *et al.*, 2010; Liang *et al.*, 2017), the logistical problems involved render these tests extremely complex to carry out. Nonetheless, whilst these field and laboratory experiments are useful for testing realistic slopes to ultimate-failure, not all important processes or failure mechanisms that operate in the field may be captured. For that reason, future studies need to take particular care to consider the best possible proxies for up-scaling and understanding ecosystem functioning.

Another way to consider scaling belowground trait data within an ecosystem or globally is to improve the representation of root form and function in terrestrial biosphere models (Warren *et al.*, 2015). Simulation modelling translates mechanistic understanding to mathematical relations that can be explored *in silico* (Marshall-Colon *et al.*, 2017). Such models range from the simulation of explicit three-dimensional root architecture and surrounding soil matrix (Dunbabin *et al.*, 2013), to more simple models scaling up trait measurements to the whole plant (Weemstra *et al.*, 2020), agricultural systems (Rosenzweig *et al.*, 2013) or the globe (Warren *et al.*, 2015). In recent years, several syntheses have called for an appropriate conceptualization of roots and their role in ecosystem functioning in terrestrial biosphere models (Smithwick *et al.*, 2014; Iversen *et al.*, 2015; McCormack *et al.*, 2015b). This approach, sometimes referred to as 'model-experiment' integration (or Mod-Ex) combines current empirical understanding with model conceptualization, parameterization, and validation in an iterative process to improve model representation of the natural world. While much work remains to be done, empirical input into the ways in which models aggregate or generalize across root functional types or plant species, and the way in which models implicitly or explicitly represent root function, can have large impacts on our understanding of ecosystem processes (Zhu *et al.*, 2016; McCormack *et al.*, 2017). In the context of crop breeding, for example, many combinations of root traits can be considered in various environments with regard to their effect on a particular function. These combinations can be validated across a restrained set of real-cases, and being used for prioritizing future research directions, similar to the use of digital prototyping in manufacturing (York, 2019). In

global biosphere and climate studies, simulation models can also aid the prioritization of research through sensitivity analyses, for example by identifying key traits whose variation have large consequences for the function of interest (McCormack *et al.*, 2015b). But, most importantly, when tested against empirical data, the results of simulations can discriminate between diverse theoretical models, or reveal (structural or context-dependent) gaps in our mechanistic representation of trait-functioning relationships (Song *et al.*, 2017).

3. Considering spatial and temporal variation

A range of methodologies have been developed above-ground, such as eddy covariance towers or remote sensing, that provide large amounts of data on certain plant traits and ecosystem functions at an ecosystem scale and across space and time. However, such approaches have low resolution regarding aspects of spatial variability in functioning and are unlikely to extend to belowground traits. Generally, there is growing evidence of strong small-scale variability in root traits (Defrenne *et al.*, 2019; Kumordzi *et al.*, 2019) that may lead to substantial small-scale variability in functioning. Given the overarching importance of soil properties and biotic (e.g. plant-plant; plant-microbes) interactions, and their typically high heterogeneity at small spatial scales (Jackson & Caldwell, 1993; Ettema & Wardle, 2002), root trait-function relationships might differ strongly over short distances (e.g. centimetres or metres). To date, it remains unclear how the spatial assemblage of species and root traits at small scales might relate to the effects estimated by species averages. Spatially aggregated data may contain little information on the range of trait values occurring within the plant community, the relative abundance of each value, or the existence of several groups of contrasting trait values (e.g. bimodal distributions of trait values), which hampers our ability to understand their consequences for the functioning of ecosystems (e.g., Valencia *et al.*, 2015; Violle *et al.*, 2017).

Likewise, soil properties vary with depth (especially when contrasting soil horizons occur) and characterizing the relative importance of roots and root traits at different depths is therefore necessary to accurately link them to plant and soil functioning (Germon *et al.*, 2016; Fort *et al.*, 2017; Chitra-Tarak *et al.*, 2019). For example, the capacity for N acquisition generally decreases with soil depth due to a decline in the availability of soil N (Wiesler & Horst, 1994; Tückmantel *et al.*, 2017). These patterns can differ across soil types and plant species: in alpine grasslands on Cambisol, the uptake of N was found to decline sharply from

67% in the top 5 cm of soil to 33% in the 5–15 cm layer below (Schleuss *et al.*, 2015), whereas it was only 44% in the top 30 cm, 32% at 30-60 cm and 24% in the 60-120 cm layer for maize in an agricultural field on Luvisol (Wiesler & Horst, 1994). Additionally, changes in trait values typically occur across contrasting soil horizons (McCormack *et al.*, 2017; Trocha *et al.*, 2017), including, for example, the typical patterns of declining root density (Jackson *et al.*, 1996) and physiological activity (Göransson *et al.*, 2008; Tückmantel *et al.*, 2017) with depth. As a consequence, most ecologists assume that (physiological, morphological, etc.) trait measurements made on roots from the topsoil are likely to adequately estimate plant N uptake capacity when N resource is concentrated in the topsoil. However, there are many reasons why such an approximation may be inadequate. First, strong competition for N in the topsoil might make root investment in deeper horizons more profitable, as sometimes observed in biodiversity studies (e.g. Mueller *et al.*, 2013), resulting in more evenly distributed resource uptake across the soil profile. Second, soil N availability interacts with other soil resources, particularly water. Seasonal fluctuations of soil water availability across the soil profile following, for example, changes in water table level and precipitation patterns may reverse the N availability gradient along the profile (Prieto *et al.*, 2012). As such, a good characterization of spatial variations in soil properties (vertically, but also sometimes horizontally; Březina *et al.*, 2019), integrated over long periods of time, might be needed to guide a sound root sampling design (and the measure of e.g., physiological and morphological traits) from the range of soil layers that matter for N uptake. Also, architectural traits or traits representing (vertical and horizontal) root distribution may be important predictors of the match between root presence and N availability (Freschet *et al.*, 2020).

There is also growing evidence that, in parallel to seasonal changes in environmental conditions, such as soil resource availability (Chitra-Tarak *et al.*, 2018; Březina *et al.*, 2019) or soil organism community composition and activity (Bardgett *et al.*, 2005), root trait values vary temporally at both the species and community levels (e.g. Picon-Cochard *et al.*, 2012; Zadworny *et al.*, 2015). For example, seasonal changes in carbohydrate concentration of below-ground organs affects plant resprouting ability during some parts of the growing season in temperate regions, a feature often used to improve the efficiency of mechanical control of weeds (Sosnová *et al.*, 2014). Many root traits are also dependent on the stage of root system development (e.g. architectural traits such as root branching density, coarse to fine root ratio; Freschet *et al.*, 2020) and root age (e.g. Volder *et al.*, 2005). Within a single root axis of maize, for example, tensile strength can vary by about 1.5 orders of magnitude, being greatest in the older root tissue far from the root apex (Loades *et al.*, 2015). This phenomenon is

particularly true for woody species, whose architecture and size can change dramatically during their life, with many consequences for trait values and their impact on ecosystem functioning. The importance of ontogenetic stage however also applies to herbaceous species (both annual and perennial) even after reaching maturity, for example due to changes in resource accumulation in roots or rhizomes. Additionally, root phenology differs strongly among species (McCormack *et al.*, 2014), growth forms (Blume-Werry *et al.*, 2016) and biomes (Abramoff & Finzi, 2014). In extreme cases, some species may display no or few absorptive roots at specific times of the year, with periodic flushes of new relatively short-lived fine roots at times of resource availability, as seen in arid climate (Liu *et al.*, 2016). In cold climate with short growing season, however, species with long-lived overwintering root systems may be more successful than species with fall-senescing root systems that are produced for each growing season anew (Courchesne *et al.*, 2020). Similarly, long-lived roots and rhizomes may contribute better to soil reinforcement against landslides than ephemeral roots by providing a more consistent contribution to improve soil strength.

A better understanding of root phenology is therefore key to the meaningful measurement of root trait values (in relation to the focal function) and our understanding of temporal variation in root trait effects on plant and ecosystem functioning. The timing of root sampling must be carefully considered, so as to match the period when the focal function is most relevant. For example, in ecosystems defined by high seasonality, measuring root traits at the peak of plant productivity (sometimes halfway between the seasonal increase and reduction in growth activities) may be a reasonable benchmark for approximating the relationship between root traits and plant nutrient uptake capacity. However, the timing of nutrient uptake is rarely examined (but see Trinder *et al.*, 2012; Jesch *et al.*, 2018; Dovrat & Sheffer, 2019) and may not be directly proportional to plant growth rate. Further, some studies suggest that N can be taken up as soon as it is available (Jackson *et al.*, 2008), suggesting that a good match between plant uptake capacity and the temporality of N fluxes is of critical importance for N uptake (e.g. Edwards & Jefferies, 2010). Regarding the capacity of plants to provide resistance against landslides, it would be best to measure root traits at the time of the year when landslides are most frequent, e.g., when soil is saturated, during the rainy season (in tropical systems) or during snow melt (Stokes *et al.*, 2009), or to differentiate between relationships measured at different times of the year.

Another consideration relates to the temporal variation in species composition within ecosystems, for example during succession or in response to changes in land use. Plant effects on ecosystem functioning can last for long periods after changes in plant community

composition have occurred (Fraterrigo *et al.*, 2005) and mismatches between traits and function are therefore likely to be observed in rapidly changing ecosystems (Foster *et al.*, 2003). In the same way, plant species, and their root systems, that established first at a location may not only influence the rooting patterns of other species, but also disproportionately drive the observed relationships between traits and functioning (Delory *et al.*, 2019).

In summary, knowledge of spatial and temporal variation in root traits and their effects, over different spatial and temporal scales, is especially needed to allow more informed recommendation on the location and timing of measurements. Hierarchical spatial sampling and sequential sampling would provide invaluable information on the spatial and temporal fluctuation of root traits and their impact on ecosystem functioning.

4. Of intra- versus interspecific variation and the use of databases

Ecologists have identified and measured phenotypic traits in a wide variety of species, either under laboratory conditions or in the field. Various attempts have been made to include these data into comprehensive/inclusive databases considering plant traits per se (Kleyer *et al.*, 2008; Iversen *et al.*, 2017; Kattge *et al.*, 2020) as well as the plant symbiotic relationships with mycorrhizal fungi (Soudzilovskaia *et al.*, 2020) and with N-fixing bacteria (Tedersoo *et al.*, 2018). Although below-ground traits are still strongly underrepresented in global compilations, especially regarding organs other than fine roots (Klimešová *et al.*, 2018), such databases represent a large amount of trait data that can be related to vegetation composition (Bruelheide *et al.*, 2019) and climate and soil maps. Consequently, relationships between root traits and ecosystem functioning can now be addressed at global scales (e.g. See *et al.*, 2019). However, in global analyses, one trait value per species is generally considered and averaged over all available data, under the assumption that the average will be a good reflection of the 'inherent' trait for a given species. This generalisation is made even though trait expression is adjusted to the specific environmental condition that plants experience (Valladares *et al.*, 2006). Root trait values can strongly differ between plants grown in laboratory versus field experiments (Poorter *et al.*, 2016), for instance as a consequence of different environmental conditions (Li *et al.*, 2017; Kumordzi *et al.*, 2019), along gradients of plant diversity or density with different types of plant-plant interactions (Salahuddin *et al.*, 2018), or with changing interactions between trophic levels (Huber *et al.*, 2016). Ostonen *et al.* (2007)

showed for example that intraspecific variation of SRL can be as high as 10-fold across a large environmental gradient. Not accounting for such differences between sites may be one of the key reasons for low predictability of trait-functioning relationships in functional ecology (Shipley *et al.*, 2016).

Due to the potential for large differences between traits and their level of intraspecific variability, getting a clearer view on which traits are most variable or invariant would be critical for data reuse in syntheses of trait-functioning relationships (Funk *et al.*, 2017; McCormack *et al.*, 2017). For above-ground traits, intraspecific variation has only recently begun to be properly addressed across large numbers of species (e.g. Siefert *et al.*, 2015). For root traits, it may be some time before we have a good insight into the contribution of genetic and environmental factors to trait variation (Klimešová *et al.*, 2017). The complexity of the issue is increased further when one considers the importance of genotype-genotype interactions of plants and root-microbial symbionts, which can also have substantial effects on trait expression and key functions (Johnson *et al.*, 2012). Overall, while the characterisation of trait intraspecific variability is critical, it must be stressed that a good characterisation of phenotypic traits also depends on a good characterisation of environmental conditions experienced by plants. This is especially true below-ground where the small-scale heterogeneity of soils limits the value of large-scale databases (Freschet *et al.*, 2017).

VI. Conclusion and perspectives

Our overview of root trait-functioning relationships has raised seven main insights:

1) Below-ground traits with the widest importance in plant and ecosystem functioning are not necessarily those that are the most commonly measured. Meanwhile, the relevance of commonly measured (soft) traits to plant and ecosystem functioning is often indirect and insubstantial, or requiring further testing.

2) Assessing the relative importance of traits for functioning requires quantifying a comprehensive range of functionally relevant traits (on different root entities), including hard traits, from a diverse range of species, as well as replication across environmental gradients or contrasting environmental contexts.

3) Establishing causal links between root traits provides a mechanistic basis (i.e. the hypothesis-based framework) to interpret the outcome of statistical model selection procedure (i.e. the set of variables retained in multivariate models linking traits to functions) or structural equation models. As such, it holds the key to identifying the most parsimonious sets of traits with strongest influence on the functions.

4) Accounting for causal relationships among traits is key to identifying the component traits that link most strongly with a limited set of genes on the one hand, and plant or ecosystem functioning on the other, and therefore to inform us of potential linkages between genotypes and functioning.

5) Investigating syndromes of traits and syndromes of trait plastic adjustments will help us identify the linkages between 'soft' and 'hard' traits, in order to demonstrate when and to what extent 'soft' traits can confidently be used as proxies for 'hard' traits.

6) Our ability to scale-up from root, to plant, to species, to community and ecosystem functioning requires more critical investigation and comprehensive experimental/empirical tests, and, in some cases, the incorporation of spatio-temporal variation as well as belowground process conceptualization and testing within the framework of terrestrial biosphere models.

7) Accounting for (the often large) intra-specific variation in trait-functioning relationships in global models requires databases with well contextualized data (e.g. locally measured soil parameters).

Another major contribution of this synthesis lies in the broad overview of root trait-function relationships gathered within Tables 1 & 2. These Tables give an overview of both the range of effects that root traits can have on ecosystem functioning and the range of traits potentially required to adequately capture the effects of roots on most plant functions and ecosystem properties and processes. They provide key references on multiple topics, which should benefit to all who want to broaden their view of root ecology. These Tables further highlight several functionally important, but rarely considered traits from various research fields.

Overall, this synthesis represents a close companion to the recent description of standardized measurement protocols for a substantial set of root traits (Freschet *et al.*, 2020).

These two syntheses elucidate connections between the multiple and at times secluded fields of root ecological research and, as such, are meant to inspire novel multidisciplinary approaches. They should encourage researchers more familiar with above-ground aspects of plant ecology to integrate below-ground concepts into their vision of trait-functioning relationships. While we purposely limited our review to below-ground aspects only, we cannot stress enough that these relationships should be considered for entire plants, whenever possible, since plant impacts on (plant and ecosystem) functioning often rely on the integration of both above- and below-ground traits.

Finally, this synthesis brings a range of arguments that call for the design of more comprehensive studies. Studies tackling some, if not all of the above recommendations can be designed that limit the fortuitous, indirect and context-dependent nature of gathered results (as opposed to studies measuring few traits on few species in one single context). We believe that such a set of recommendations will be instrumental in moving towards an integrated, mechanistic knowledge of trait-functioning relationships and open the way to safe applications for ecosystem and agroecosystem management. Achieving a more mechanistic understanding of multivariate trait-functioning relationships will further help us strengthen (or reconsider) the foundations of current dominating theoretical frameworks, often built on data from few soft traits.

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Author contributions

GTF initiated and coordinated the writing of the manuscript. GTF, CR, MW and AS organized the Workshop and chaired the sessions, with help from LHC. GTF, CR, LHC, MW, GB, BR, RDB, GBD, DJ, JK, ML, MLM, ICM, LP, HP, IP, NW, MZ and AS participated in the Workshop. GTF, CR, AS, MW, GB, LHC, BR, HP, JK, IP, NW, CMI and LY drafted some parts of the manuscript and all authors, including AB-Z, EBB, IB, AG, SEH, LM, CP-C, JAP, LR, PR, MS-L, NAS, TS, OJV and AW, contributed to the writing of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1. Full list of references for papers cited in Tables 1, 2, 3 & 4.

Tables

Table 1. Broad, multidisciplinary assessment of theoretical and demonstrated links between below-ground traits and 15 aspects of plant functioning.

PLANT FUNCTIONS				
CC	Belowground traits	Entity of interest	References (examples of)	Rationale
Soil space occupancy (from explorative to exploitative strategies)				This function includes both exploration and exploitative strategies (whose traits generally trade-off).
	Maximum rooting depth* (explorative)	Whole root system	Thorup-Kristensen, 2001; Maeght *et al.*, 2013; Fan *et al.,* 2017	Reflects the potential range of soil layers colonized by roots.
	Lateral rooting extent* (explorative)	Whole root system	Schenk & Jackson, 2002a	Reflects the potential area of ground colonized by roots.
	Horizontal* and vertical root distribution index* (explorative)	Whole root system, fine-roots	Gale & Gringal, 1987; Jackson *et al.,* 1996	A homogeneous distribution below the soil surface and across depths is typical of an explorative rather than an exploitative strategy.
	Root length density* (exploitative)	Whole root system, fine-roots	Eissenstat, 1992; Robinson *et al.*, 1994; Reich *et al.,* 1998; Ravenek *et al.,* 2016	Increases the spatial coverage of a given soil volume.
	Root mass fraction* (exploitative)	Whole root system, fine-roots	Poorter *et al.,* 2012; Freschet *et al.,* 2015	Increases the proportional investment of plants towards the root system or specific parts of the root system.
	Specific root length* (explorative or exploitative)	Whole root system, fine-roots	Bauhus & Messier, 1999; Ostonen *et al.,* 2007	Increases the length of root exploring or exploiting the soil per unit root mass invested.
	Root branching density* (exploitative)	Whole root system, absorptive roots	Wiersum, 1958; Fitter & Stickland 1991; Larigauderie & Richards, 1994; Eissenstat *et al.,* 2015; Zhao *et al.*, 2018 ; Lynch *et al.*, 2019	Typically increases with soil resource patchiness as very thin roots tend to proliferate (strong increase in root branching density) in nutrient-rich hotspots. While higher branching density increases local soil exploitation, lower branching might enable larger soil volume exploration.

	Root elongation rate* (explorative or exploitative)	First-order roots	Forde & Lorenzo 2001; Rewald & Leuschner, 2009; Eissenstat *et al.,* 2015	On pioneer roots, measures the capacity of root systems to send roots to depth (explorative). On absorptive roots, characterizes the capacity of root systems to respond to fluctuating resource availability (exploitative).
	Time of root growth initiation*	First-order roots	Langlois *et al.*, 1983; Eissenstat & Caldwell, 1988	Measures the capacity of root systems to pre-occupy soil patches before competitors.
	Root branching angle* (explorative)	Highest order roots	Trachsel *et al.,* 2013; Lynch, 2013; Miguel *et al.*, 2015	Larger (i.e. steeper) root branching angles promote exploration of deep soil and increase soil volume explored in conditions of competition with neighbouring plants.
	Persistence of connection between ramets* (explorative)	Rhizomes, stolons, shoot-bearing roots	Jónsdóttir & Watson, 1997; Weiser *et al.,* 2016; Klimešová *et al.*, 2018	Longer lifespan of rhizomes and shoot bearing roots enables sharing of resources among ramets in a clone over longer period and larger area and enables also longer on-spot occupancy. Longer persistence of connections is also generally related to longer root lifespan.
	Lateral spread* (explorative)	Rhizomes, stolons, shoot-bearing roots	Weiser & Smyčka, 2015; Klimešová *et al.*, 2018	The longer lateral spread by clonal growth organ (stolon, rhizome) the farther away (from older roots) new roots must be established.
Plant N acquisition				
	See traits associated to "Soil space occupancy" (+)	Whole root system, absorptive roots	Maire *et al.,* 2009; Simon *et al.*, 2017; Freschet *et al.,* 2018	Most "Soil space occupancy" traits can be important for this function as they determine the temporal and spatial localisation of roots in soil and the efficiency of soil exploration and exploitation.
	Net N uptake rate* (+)	Whole root system, absorptive roots	Garnier, 1991; Poorter *et al.,* 1991; Garnier *et al.,* 1998	When measured on short time periods (from hours to days), this measure primarily represents plant N uptake. Over longer periods (days to months) this measure also takes into account N loss due to leaching, herbivory and senescence.
	Michaelis-Menten constant (Km)* (+)	Whole root system, absorptive roots	Robinson *et al.,* 1994; Miller *et al.*, 2007; Grassein *et al.,* 2015	The Km is a measure of the affinity of a transport system for its substrate; the lower the Km the faster nutrients can be taken up at low availability.
	Ability to fix N* (+)	Nodules	Sprent, 2009; Afkhami *et al.,* 2018; Tedersoo *et al.,* 2018	Provides N to the plant from atmospheric source N_2 via microbial root symbionts.
	Nitrogen fixation rate* (+)	Nodules	Carlsson & Huss-Danell, 2003; Batterman *et al.,* 2013a; Yelenik *et al.,* 2013; Ament *et al.,* 2018	Increases the rate of atmospheric N acquisition.
	Mycorrhizal association type*	Absorptive roots	Read & Perez Moreno, 2003; Read *et al.,* 2004; Lambers *et al.*, 2009; Phillips *et al.,* 2013; Liese *et al.*, 2018; Pellitier & Zak, 2018	Different mycorrhizal types have different enzymatic capacities and ability to explore soil volumes and thereby different abilities to take up N. Also, AM, ECM, and ERM fungi represent a gradient from limited saprotrophic capabilities and greater reliance on inorganic N as primary N source to the ability to produce extracellular enzymes and greater use of increasingly complex organic N forms.
	Root hair length* and density* (+)	Absorptive roots	Robinson & Rorison, 1987; Freschet *et al.,* 2018	Root hairs increase the absorptive surface area of non-woody roots, which is important for N uptake as well as uptake of other nutrients.
	Ratio of absorptive to transport roots* (+/-)	Fine-roots	Schneider *et al.*, 2017; Zadworny *et al.*, 2017	Increases N uptake rate. However, root cortical senescence can also increase N reallocation from senescing tissue and reduce root respiration and root N requirements.

	Mycorrhizal colonization intensity* (+)	Absorptive roots	Miller *et al.*, 1995; Hodge *et al.,* 2003; Treseder, 2013	Mycorrhizal fungi are physiologically and morphologically well-adapted to acquire N from soil. The colonization intensity provides a first approximation of the association between the plant and mycorrhizal partner. However, it should be noted that there is still significant variation in the potential benefit provided by the fungi based on the fungi identity, the total hyphal production and the local environmental context.
	Root cortical aerenchyma (+/-)	Absorptive roots	Postma & Lynch, 2011; Schneider *et al.*, 2017	Decreases radial N transport but increases nutrient uptake efficiency by decreasing metabolic costs.
	Maximum net uptake capacity (Imax)* (+)	Absorptive roots	Robinson *et al.,* 1994; Garnier *et al.,* 1998; Grassein *et al.,* 2018	Imax represents a potential rate at non-limiting substrate availability that might, however, not be fully expressed under in situ conditions.
	Mycorrhizal hyphal length (+)	Absorptive roots	Miller *et al.*, 1995; Chen *et al.*, 2016; McCormack & Iversen, 2019	The hyphal length associated with a colonized root provides a closer approximation of both the potential benefit and cost of the mycorrhizal symbiosis than colonization intensity alone.
	Specific root respiration* (+)	Absorptive roots	Poorter *et al.,* 1991; Reich *et al.,* 1998; Rewald *et al.*, 2016	Root respiration is related simultaneously to maintenance, growth and nutrient uptake of roots and is therefore inconsistently linked to nutrient uptake. It also varies with N form.
	Root N concentration (+)	Absorptive roots	Loqué & von Wirén, 2004; Grassein *et al.,* 2015; Grassein *et al.,* 2018	Root nitrogen is involved in all metabolic processes related to N uptake but is also stored in roots and included in root defence compounds and is therefore inconsistently linked to nutrient uptake.
Plant P acquisition				
	See traits associated to "Soil space occupancy" (+)	Whole root system, absorptive roots	Lynch *et al.,* 2011; Laliberté *et al.,* 2015; Ros *et al.,* 2018	Most "Soil space occupancy" traits can be important for this function.
	Net P uptake rate* (+)	Whole root system, absorptive roots	Itoh, 1987; Föhse *et al.*, 1988	When measured on short time periods (from hours to days), this measure primarily represents plant P uptake. Over longer periods (days to months) this measure also takes into account P loss due to leaching, herbivory and senescence.
	Mycorrhizal association type*	Absorptive roots	Read, 1991; Read & Perez-Moreno, 2003; Philipps *et al.,* 2013; Lambers *et al.*, 2009	Distinct mycorrhizal types have differing capacity to extract P from soils. AM fungi have greater influence on plant P acquisition (representing up to 90% of plant P uptake) than ECM fungi (up to 70%). AM fungal extramatrical mycelia express specific transporters to take up P_i from the periarbuscular space (i.e., they bypass roots). ECM and ERM fungi can access organic forms of P that are not available to AM fungi.
	Ability to grow cluster and dauciform roots (+)	First-order roots	Neumann & Martinoia, 2002; Shane *et al.,* 2006	Cluster and dauciform roots are specialized organs efficient in mining P from nutrient-impoverished soils.
	Root hair length* and density* (+)	Absorptive roots	Wissuwa & Ae, 2001; Brown *et al.,* 2013; Haling *et al.,* 2013	Root hairs can be more effective than mycorrhiza in facilitating P acquisition.
	Ratio of absorptive to transport roots* (+/-)	Fine-roots	Schneider *et al.*, 2017; Zadworny *et al.*, 2017	Increases P uptake rate. However, root cortical senescence can also increase P reallocation from senescing tissue and reduce root respiration and root P requirements.
	Rhizospheric phytase and phosphatase activity (+)	First-order roots	Spohn & Kuzyakov, 2013; Meier *et al.,* 2015	Roots can release (acid) phosphatases (sometimes phytases) directly or exude organic substances that act as substrate for microorganisms which in turn produce phytases and (acid or alkaline) phosphatases.
	Mycorrhizal colonization intensity* (+)	Absorptive roots	Treseder, 2013; Elumeeva *et al.,* 2018	Mycorrhizal fungi are physiologically and morphologically better adapted than roots to extract P from soils thereby increasing host plant nutrient concentrations.

	Mycorrhizal genetic diversity* (+)	Absorptive roots	Plassard & Dell, 2010; Plassard *et al.,* 2011; Köhler *et al.,* 2018	P uptake efficiency increases with increasing ECM fungi species richness and diversity. Increased ECM fungi diversity is associated with greater variability in soil exploration types among ECM fungi species, which increases the explored soil volume for P.
	Root cortical aerenchyma (+/-)	Absorptive roots	Hu *et al.*, 2014; Schneider *et al.*, 2017	Decreases radial P transport but increases nutrient uptake efficiency by decreasing metabolic costs.
	Root exudation rate* (+)	Absorptive roots	Lopez-Bucio *et al.,* 2000; Lambers *et al.,* 2012; Ryan *et al.,* 2014; Zhang *et al.,* 2016	Excretion of acidifying/chelating compounds (e.g., citric acid, malic acid) enhances the solubility of inorganic P, although evidence exists mostly for Proteaceae and crops.
	Mycorrhizal hyphal length (+)	Absorptive roots	Miller *et al.*, 1995; Laliberté *et al.*, 2015; Chen *et al.*, 2016; McCormack & Iversen, 2019	The amount of hyphal length associated with a colonized root provides a closer approximation of both the potential benefit and cost of the mycorrhizal symbiosis than colonization intensity alone.
	Michaelis-Menten constant (Km)* (+)	Whole root system, absorptive roots	Itoh, 1987; Lambers *et al.*, 2006	The Km is a measure of the affinity of a transport system for its substrate; the lower the Km the faster nutrients can be taken up at low availability. However, the diffusion of inorganic phosphate in soil is the key limiting factor for P uptake so that kinetic parameters of the P-uptake system may have only small effects on the overall uptake capacity of plants.
Plant water acquisition				
	See traits associated to "Soil space occupancy" (+)	Whole root system, absorptive roots	Fort *et al.,* 2017; Chitra-Tarak *et al.*, 2019	Most "Soil space occupancy" traits can be important for this function, especially in soils with heterogeneous water distribution.
	Root hair length* and density* (+)	Absorptive roots	Segal *et al.*, 2008; Carminati *et al.,* 2017	Improve the contact of roots with water films of soil particles.
	Cortical thickness* (-)	Absorptive roots	Huang & Eissenstat, 2000; Comas *et al.,* 2012	Thinner cortex resulting in less impedance to water movement towards the stele.
	Fraction of passage cells in exodermis* (+)	Absorptive roots	Enstone & Peterson, 1992; Peterson & Enstone, 1996; Huang *et al.,* 1995; Peterson & Waite, 1996	Higher density of passage cells enhances water movement towards the stele.
	Mycorrhizal colonization intensity* (+)	Absorptive roots	Augé *et al.,* 2001; Querejeta *et al.,* 2003; Querejeta *et al.,* 2012; Prieto *et al.,* 2016	Allows water transfer to the plant and improves root contact with the soil.
	Hydraulic conductance* (+)	Whole root system, fine-roots	Muhsin & Zwiazek, 2002; Eldhuset *et al.,* 2013; Zadworny *et al.,* 2018	Increases the potential flow of water from the roots to upper parts of the plant.
	Vulnerability to embolism (-)	Whole root system	Domec *et al.*, 2006	Occurrence of embolism limits the potential flow of water from roots to upper parts of the plant
	Type and frequency of root entities	Whole root system	North, 2004; Draye *et al.*, 2010; Rewald *et al.*, 2011, 2012; Ahmed *et al.*, 2018	Distribution of the root hydraulic properties between root entities determines root system hydraulic architecture.
	See traits associated to "Soil water holding capacity" (+)	Fine-roots	Feddes *et al.*, 2001	Soil water holding capacity acts as a buffer against periodic rainfall events, particularly in places where rainfall evens are irregular.
	Suberin concentration (-)	Whole root system	Steudle & Peterson, 1998; Schreiber *et al.,* 2005; Gambetta *et al.,* 2013	Not only deposition of suberin lamellae but also chemical composition of suberin would affect radial water flow from cell to cell (i.e. decrease root hydraulic conductivity).

	Xylem lumen area (+)	Whole root system, fine-roots	Hummel *et al.,* 2007; Valenzuela-Estrada *et al.,* 2008; Long *et al.,* 2013; Kong *et al.,* 2014	Greater conduit lumen area may exhibit enhanced hydraulic conductance.
	Aquaporin expression (+)	Absorptive roots	Johnson *et al.*, 2014	Facilitates radial, symplastic conductance of water.
	Lignin concentration* (-)	Absorptive roots	Ranathunge *et al.,* 2003, 2004; Naseer *et al.,* 2012	Lignins may act as apoplastic barriers limiting radial water transport across roots.
Root penetration of soil				
	Root growth pressure (+)	First-order roots	Dexter, 1987; Clark & Barraclough, 1999	Root growth pressure is essential to root penetration, although there is limited evidence of its variation as a trait.
	Mean root diameter* (+)	First-order roots	Materechera *et al.,* 1992	Thicker roots are generally better at penetrating hard soils to greater depth.
	Number of main root axes (+)	Whole root system	Jakobson & Dexter, 1987; Landl *et al.,* 2017	In structured soils containing many cracks and biopores, plants with many main axes may penetrate more effectively.
	Root buckling resistance (+)	First-order roots	Clark *et al.,* 2008; Burr-Hersey *et al.,* 2017	Species and genotypes differ substantially in their ability to penetrate hard soils without buckling or altering their growth trajectory.
	Root cap friction coefficient (-)	First-order roots	Bengough & McKenzie, 1997; Iijima *et al.,* 2003	Sloughing of root border cells and root exudate production decreases the mechanical resistance to root growth and aids root penetration.
Plant nutrient and C conservation				
	Lifespan* (+)	Whole root system, rhizomes	McCormack *et al.,* 2012; Liu *et al.,* 2016; Klimešová *et al.,* 2018	Decreases losses associated to root turnover.
	Root resorption efficiency and proficiency (+)	Whole root system, absorptive roots	Gordon & Jackson, 2000; Freschet *et al.,* 2010	Decreases losses associated to root senescence.
	Specific respiration rate* (-)	Whole root system	Walk *et al.*, 2006; Rewald *et al.*, 2014, 2016	Respiration is a major driver of C loss.
	Ratio of absorptive to transport roots* (-)	Fine-roots	Lynch, 2019; Schneider *et al.*, 2017	Root cortical senescence reduces metabolic maintenance costs.
	See traits associated to "Plant protection against pathogens and herbivory" (+)	Whole root system	Kaplan *et al.,* 2008; Moore & Johnson, 2017	Traits providing "Plant protection against pathogens and herbivory" are important for this function.
	Root tissue density* (+)	Whole root system	Ryser, 1996; Liu *et al.,* 2016; Bumb *et al.,* 2018; Lynch, 2019	Increases root lifespan, plant mechanical resistance and decreases plant palatability. Evidence gathered aboveground for leaf tissue density (e.g. leaf dry matter content) theoretically applies belowground. However, reduced tissue density due to aerenchyma formation, increase in cortical cell sizes or decrease in cortical cell numbers may also reduce metabolic costs.
Plant storage				
	Ability to produce storage structures (+)	Tubers, rhizomes, tap roots, corms, bulbs	Klimešová *et al.*, 2018; Pausas *et al.*, 2018	Substantially improves the overall capacity of plants to store C and nutrients.
	Total belowground carbohydrate storage* (+)	Tubers, rhizomes, tap roots, corms, bulbs	Janeček & Klimešová, 2014; Martínez-Vilalta *et al.,* 2016	Storage in specialized organs represents the largest part of C storage and, in contrast to storage in other types of roots, represents an active storage strategy rather than passive accumulation due to limitation of growth (e.g. by nutrients, cold).

Plant regeneration				
	Bud bank size* (+)	Whole root system, rhizomes	Klimešová & Klimeš, 2007; Ott *et al.*, 2019	Belowground bud bank allows plant regeneration after aboveground disturbance
	Depth of buds in bud bank (+)	Whole root system, rhizomes	Lubbe & Henry, 2019; Ott *et al.*, 2019	Deeper buds are more resistant to disturbance like fire or ploughing. On the other hand, deeper buds require more resource storage and time to produce new aboveground shoots.
	See traits associated to "Plant storage" (+)	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016	Most "Plant storage" traits can be important for this function. Storage organs support regrowth of new aboveground parts.
	Ability to produce adventitious shoots on roots (+)	Whole root system	Klimešová *et al.,* 2017a	Adaptation of plants to soil disturbance (numerous perennial weeds of arable land possess ability to resprout from roots). Some species may produce adventitious shoots spontaneously, some only in response to disturbance.
Plant lateral spread and belowground dispersal				
	Ability to produce rhizomes (+)	Rhizomes	Groff & Kaplan, 1988	Rhizomes (belowground stems with adventitious roots) allow the colonization of new ground while relying to some extent on resources from well-established ramets.
	Lateral spread* (explorative)	Rhizomes, stolons, shoot-bearing roots	Weiser & Smyčka, 2015; Klimešová *et al.*, 2018	The longer lateral spread by clonal growth organ (stolon, rhizome) the farther away (from older roots) new roots must be established.
	Ability to produce adventitious roots (+)	Whole root system, rhizomes	Groff & Kaplan, 1988	Facilitates establishment of new rooted areas along belowground (rhizomes) or aboveground (stolons, decumbent shoots) stems and splitting a clone to physically independent parts.
	Lateral rooting extent* (explorative)	Whole root system	Schenk & Jackson, 2002a	Reflects the potential area of ground colonized by roots.
	Ability to produce adventitious shoots on roots (+)	Shoot-bearing roots	Groff & Kaplan, 1988; Klimešová *et al.,* 2017a	Common among species of dry and disturbed areas to extend plant spread and to overcome bud bank limitation.
	See traits associated to "Plant storage" (+)	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016; Klimešová *et al.,* 2017b	Most "Plant storage" traits can be important for this function as they often serve both functions.
	See traits associated to "Root penetration force in soil" (+)	Root and rhizome apices	Klimešová *et al.*, 2012	Facilitates movement of roots and rhizomes into new areas.
	Persistence of connection between ramets* (+)	Rhizomes, shoot bearing roots	Jónsdóttir & Watson, 1997	Longer lifespan of rhizomes and shoot bearing roots enables sharing of resources among ramets in a clone over a longer period and larger area and enables longer on-spot occupancy.
Initiation and establishment of mycorrhizal symbioses				This function refers to mycorrhizal fungi as well as pathogenic hyphae.
	Root cortex thickness* (+)	Absorptive roots	Brundrett, 2002; Comas *et al.,* 2012; Zadworny *et al.,* 2016; Kong *et al.,* 2017	Larger parenchyma cortex enhances associations with mycorrhizal colonization by providing larger space for mycorrhizal fungal hyphae and arbuscules.
	See traits associated to "Plant P acquisition" (-)	Absorptive roots	Oldroyd, 2013; Raven *et al.,* 2018	Most "Plant P acquisition" traits can be important for this function. Plants with higher P acquisition capacities and therefore higher P status are less likely to establish symbioses.
	Root cortex area fraction* (+)	Absorptive roots	Comas *et al.,* 2012; Burton *et al.,* 2013; Gu *et al.,* 2014; Valverde-Barrantes *et al.,* 2016	A large cortex area fraction theoretically implies a higher possibility for connection to symbionts by providing larger space for mycorrhizal fungal hyphae and arbuscules.

	Fraction of passage cells in exodermis* (+)	Absorptive roots	Kamula *et al.,* 1994; Peterson & Enstone, 1996; Sharda & Koide, 2008; Zadworny & Eissenstat, 2011	Exodermal passage cells provide the major penetration sites for the colonization of mycorrhizal and pathogenic hyphae.
	Concentration of compounds controlling the degree of colonization: e.g. lignin, suberin, phenolic compounds, phytohormones, 'reactive oxygen species', branching factors (-)	Absorptive roots	Nicholson & Hammerschmidt, 1992; Matern *et al.,* 1995; Fester & Hause 2005; López-Ráez *et al.,* 2010	Roots contain and produce anti-fungal compounds (i.e. lignin deposition, suberization, high tannin content and 'reactive oxygen species') that control fungi (pathogenic and mycorrhizal) entry and development.
	Carbon translocation to symbionts (+)	Whole root system	Tuomi *et al.,* 2001; Hogberg & Hogberg, 2002; Hobbie, 2006; Nehls *et al.,* 2010	Symbiosis establishment require plant resources such as photosynthetically assimilated carbon; the symbiosis affects the rate of photosynthesis and influences the carbon assimilation and allocation
Plant protection against pathogens and herbivory				
	Secondary metabolites (alkaloids, glucosinolates, phenolics, terpenoids, furanocoumarins, cardenolides) (+)	Whole root system, absorptive roots	Zangerl & Rutledge, 1996; Bezemer *et al.,* 2004; Kaplan *et al.,* 2008; Rasmann *et al.,* 2009; Moore & Johnson, 2018	Decreases plant palatability.
	Mycorrhizal colonization intensity* (+)	Absorptive roots	Newsham *et al.,* 1995; Jung *et al.,* 2012; Babikova *et al.,* 2014	Provides protection against some herbivores and pathogens.
	Fraction of passage cells in exodermis* (-)	Absorptive roots	Kamula *et al.*, 1994	Exodermal passage cells provide the major penetration sites for the colonization of pathogenic fungi.
	See traits associated to "Plant resistance to uprooting" (+)	Whole root system	Ennos, 2000; Burylo *et al.,* 2009	Prevents uprooting during grazing by aboveground herbivores and total root system disruption during grazing by belowground herbivores.
	Root lignin concentration* (+)	Whole root system, absorptive roots	Johnson *et al.,* 2010	Lignin concentration and composition contribute to root toughness acting as an effective barrier to root herbivory.
	Root silica and calcium oxalate content (+)	Absorptive roots	Korth *et al.,* 2006; Park *et al.,* 2009; Moore & Johnson, 2017	These deposits are hard and can abrade insect mouthparts and reduce the digestibility of food via a physical action.
	Root tissue density* (+)	Whole root system, absorptive roots	Bumb *et al.,* 2018	Decreases plant palatability. Evidence gathered aboveground for leaf tissue density (e.g. leaf dry matter content) theoretically applies belowground.
	Root N concentration* (-)	Whole root system, absorptive roots	Brown & Gange, 1990; Dawson *et al.,* 2002; Agrawal *et al.,* 2006	Low levels of N limit the nutritional value of the root tissue, as evidenced aboveground.
	Root hair length* and density* (+)	Absorptive roots	Johnson *et al.,* 2016; Moore & Johnson, 2017	Root hairs offer some protection by preventing very small herbivores from reaching and penetrating the root epidermis or by providing refuge for natural enemies of herbivores such as entomopathogenic nematodes.
Plant resistance to vertical uprooting				This applies particularly to herbaceous species (e.g. under conditions of large herbivore grazing).
	Root length density* (+)	Whole root system	Ennos, 1989.	Particularly important across a range of soil horizons. Increasing root length augments the pull-out resistance up to a critical root axis length, above which roots will break in tension instead of slipping out of the soil.
	Root mass fraction* (+)	Whole root system	Ennos, 1993	Low investment in belowground parts increases chances of uprooting.

	Root branching density* (+)	Whole root system	Dupuy *et al.,* 2005a; Devkota *et al.,* 2006; Burylo *et al.,* 2009	The tensile force required to uproot whole plants is positively related to the root branching density and number of root tips per unit volume of soil.
	Tensile strength* (+)	Whole root system	Ennos & Pellerin, 2000; Chimungu *et al.,* 2015; Mao *et al.,* 2018	An estimation of total anchorage strength can be obtained by summing the basal tensile strengths of all the roots.
	Modulus of elasticity* (-)	Whole root system	Mao *et al.,* 2018	If a root has a small elastic modulus, it will be able to deform further without failing under a given load, thus improving plant anchorage.
	Ability to produce rhizomes (+)	Rhizomes	Bankhead *et al.,* 2017	The force required to cause rhizome failure can be high, thus improving overall plant anchorage.
	Lateral rooting extent* (+)	Whole root system	Ennos, 1989; Mickovski *et al.,* 2005	Lateral roots increase the weight of the root-soil plate enmeshed by roots. Increasing root length augments the pull-out resistance up to a critical root axis length, above which roots will break in tension instead of slipping out of the soil.
	Specific root length (+)	Whole root system	Ennos, 1993; Edmaier *et al.,* 2015	High specific root length often implies more numerous thinner roots improving anchorage whereas low specific root length implies less but thicker roots.
Plant resistance to overturning				This function applies particularly to tree species (e.g. under conditions of lateral wind loading).
	Root area ratio (+)	Whole root system	Dupuy *et al.,* 2005b	The greater the root area ratio of coarse and fine roots (although roots > 2 cm in diameter contribute less) crossing the potential failure zone (edges of soil-root plate), the more the soil shear strength is increased around the root-soil plate.
	Vertical root length distribution index* (+)	Whole root system	Bruce *et al.,* 2006; Fourcaud *et al.,* 2008	Deeper root systems are better anchored because the anchorage force provided by roots is proportional to their length up to a critical length, beyond which roots will break before more distal regions are stretched.
	Root length density* (+)	Whole root system	Danquechin Dorval *et al.,* 2016	The higher the density of roots, either tap, sinker or lateral roots, the greater the resistance to overturning.
	Root mass fraction* (+)	Whole root system	Danquechin Dorval *et al.,* 2016	Proportionally low investment in below-ground parts increases chances of overturning.
	Root bending strength (+)	Lateral roots, sinker roots	Nicoll & Ray, 1996; Stokes & Mattheck, 1996	Increases resistance to failure due to root bending during lateral sway.
	Presence of sinker roots along lateral roots (+)	Lateral roots	Danjon *et al.,* 2005	Sinker roots capture a mass of soil and so increase the weight of the root-soil plate. During lateral sway, a heavier root-soil plate will improve resistance to overturning.
	Presence of a taproot (+)	Taproot	Ennos, 1993; Fourcaud *et al.,* 2008; Burylo *et al.,* 2010; Yang *et al.,* 2017	If shallow lateral roots are growing horizontally from the taproot, then the taproot constitutes the main root element that contributes to anchorage rigidity. Longer taproots anchor the plant better in soil.
Plant tolerance to waterlogging				
	Presence of aerenchyma tissue (+)	Absorptive roots, adventitious roots, rhizomes	Kohl *et al.*, 1996; Colmer, 2003; Colmer & Voesenek, 2009; Abiko *et al.,* 2012; Sauter, 2013	Improves root tissue oxygenation by conducting air along the roots (and rhizomes).
	Presence of pneumatophores (+)	Pneumatophores	Purnobasuki & Suzuki, 2005; Zhang *et al.,* 2015; da Ponte *et al.,* 2019	Pneumatophores (i.e. aerial roots) are morpho-anatomical adaptations of roots with negative geotropism that emerge above the water surface to take up oxygen.

	Root tissue porosity (+)	Whole root system	Gibberd *et al.,* 2001; Purnobasuki & Suzuki, 2004; Ding *et al.,* 2017; Striker & Colmer, 2017	Enhances the internal movements of gases and increases root oxygenation in anaerobic soils.
	Tolerance to high ethanol concentration (+)	Whole root system	Jackson *et al.,* 1982; Boamfa *et al.,* 2005; Maricle *et al.,* 2014	Ethanol toxicity is a prime cause of the injury and death of flooded plants.
	Fine root regrowth rate (+)	Whole root system	Vidoz *et al.,* 2010; Luo *et al.,* 2011; Sauter 2013; Dawood *et al.,* 2014	Adventitious roots functionally replace primary root systems that may deteriorate during flooding due to oxygen deficiency.
	Specific root respiration* (-)	Whole root system	Moog & Brugemann, 1998; Nakamura & Nakamura, 2016	Reduces root oxygen requirements.
Plant resistance to and avoidance of drought				
	Critical tension for conduit collapse* (+)	Whole root system	Hacke *et al.,* 2001	Decrease the risk of conduit collapse during drought.
	See traits associated to "Plant water acquisition" (+)	Whole root system, absorptive roots	Brunner *et al.*, 2015	Most "plant water acquisition" traits, including "soil space occupancy" traits, are important for plant resistance to drought.
	See traits associated to "Plant regeneration" (+)	Whole root system, tubers, rhizomes, tap roots, corms, bulbs	Qian *et al.*, 2017	Plant regeneration capacity provides plants with the ability to survive intense drought periods despite the loss of aboveground biomass.
	See traits associated to "Plant storage" (+)	Tubers, rhizomes, tap roots, corms, bulbs	de Moraes *et al.*, 2016	Most "Plant storage" traits can be important for this function. Storage organs support regrowth of new aboveground parts.

CC: colour code, in dark blue: trait of prime importance for performing the plant function in at least some environmental conditions; medium blue: trait of secondary importance in at least some environmental conditions; light blue: trait of potential but unknown importance due to missing or low experimental evidence. * refers to traits whose measurement protocols are described in Freschet *et al.* (2020). (+) versus (-) refers to the positive or negative effect of one trait on the function, respectively. (explorative) versus (exploitative) refers to traits that increase the overall volume of soil explored or improve the exploitation of a more limited volume of soil, respectively. 'Entity of interest' refers to a range of plant belowground parts as described in Freschet *et al.* (2020). The full list of references is available as Supplementary Notes S1.

Table 2. Broad, multidisciplinary assessment of theoretical and demonstrated links between below-ground traits and nine aspects of ecosystem functioning.

ECOSYSTEM PROCESSES AND PROPERTIES				
CC	Belowground traits	Entity of interest	References (examples of)	Rationale
Ecosystem C cycling				This process includes C inputs, losses, retention and transformation. Its complexity may not be meaningfully simplified into traits that accelerate versus decelerate the element cycling.
	See traits associated to "Soil space occupancy"	Whole root system, absorptive roots, rhizomes	Jastrow *et al.,* 1998; Jobbagy & Jackson, 2000; Rasse *et al.*, 2005; De Deyn *et al.*, 2008; Wang *et al.*, 2010; Clemmensen *et al.*, 2013; Pérès *et al.,* 2013; Cornelissen *et al.,* 2014; Liao *et al.*, 2014; Gould *et al.,* 2016; Poirier *et al.,* 2018	Most "Soil space occupancy" traits can be important for this process because they determine the location (i.e. biotic and abiotic conditions) of root effects on soil, influences the amount of contact surface between roots and soil (e.g. physical enmeshment of soil aggregates), influences the amount of root-derived C inputs to soil (e.g. litter, exudates), soil moisture and nutrient availability.
	Mycorrhizal association type*	Absorptive roots	Langley *et al.,* 2006; Phillips *et al.,* 2013; Averill *et al.,* 2014; Soudzilovskaia *et al.,* 2015, 2019	Ecosystems dominated by arbuscular mycorrhizal, ericoid mycorrhizal and ectomycorrhizal fungi plants are characterized by different carbon and mineral nutrient cycles due to the different enzymatic capacities of the symbionts. Ecosystems dominated by plants in symbiosis with ectomycorrhizal fungi store 70% more C in soils than ecosystems dominated by arbuscular mycorrhizal-associated plants.
	Specific root respiration*	Absorptive roots	Bond-Lamberty *et al.*, 2004; Reich *et al.*, 2008; Bardgett *et al.,* 2014	The contribution of root respiration represents on average 40-50% of the total soil CO_2 efflux but varies strongly among species.
	Mycorrhizal colonization intensity*	Absorptive roots	Rillig *et al.,* 2001; Gleixner *et al.,* 2002; Kögel-Knabner, 2002; Allen *et al.,* 2003; Langley & Hungate, 2003; Fernandez *et al.*, 2016; Poirier *et al.,* 2018	Mycorrhizal fungi synthesize hydrophobic and recalcitrant compounds, such as chitin and melanin, respectively, which are discussed to be less biodegradable and to accumulate in soils (at least in ecosystems experiencing cold climates).
	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.,* 1997; Fan & Guo, 2010; McCormack *et al.,* 2015; Klimešová *et al.*, 2018	Root lifespan regulates the quantity and quality of root-derived organic matter transferred into the soil organic matter pool. Fine-roots and low-order roots, which have a short lifespan and turnover rapidly, represent a substantial input of C into the soil.
	Root litter mass loss rate*	Whole root system, fine-roots	Silver & Miya, 2001; Zhang & Wang, 2015; See *et al.*, 2019	Determines the rate at which C from litters is released into the atmosphere or enters the soil in the form of particulate organic matter or dissolved organic matter.
	Root exudation rate*	Fine-roots	Tisdall & Oades, 1982; Kuzyakov, 2010; Phillips *et al.,* 2011; Keiluweit *et al.,* 2015; Tückmantel *et al.,* 2017; Henneron *et al.*, 2020	Enhanced root exudation increases the microbial activity and accelerates the breakdown of soil organic matter in the rhizosphere (priming effect). Meanwhile root exudates can act as binding agents to stabilize soil aggregates and thus enhance the stabilization of occluded soil organic matter.
	Root hair length and density*	First-order roots	Gould *et al.,* 2016; Poirier *et al.,* 2018	Root hairs can physically attach soil particles and contribute to the formation of stable soil aggregates enriched in C.
	Mycorrhizal hyphal length	Absorptive roots	Miller & Jastrow, 1990; Degens, 1997; Wilson *et al.,* 2009; Wu *et al.,* 2014	Increased hyphal length leads to greater enmeshment of soil particles and increases soil aggregate stability and soil organic C stabilisation.

	Ability to fix N*	Nodules	Cole *et al.,* 1995; Binkley, 2005; Kaye *et al.,* 2000; Fornara & Tilman, 2008; De Deyn *et al.,* 2011	The biological fixation of N_2 by N_2-fixing root symbiotic bacteria generally increases the plant belowground and aboveground primary productivity. The presence of N_2-fixing species also tends to increase soil organic C accumulation.
	Root branching density*	Absorptive roots	Poirier *et al.,* 2018	A high branching density contributes to stabilizing soil aggregates through enmeshment of soil particles and higher production of exudates by root tips.
	See traits associated to "Hydraulic redistribution" (+)		Domec *et al.*, 2010	Affects topsoil organic matter and litter decomposition.
Ecosystem N cycling				This process includes N inputs, losses, retention and transformation. Its complexity may not be meaningfully simplified into traits that accelerate versus decelerate the element cycling.
	See traits associated to "Soil space occupancy"	Whole root system, absorptive roots	Fornara *et al.,* 2011; Abalos *et al.,* 2014; De Vries *et al.,* 2016	Most "Soil space occupancy" traits can be important for this process. The density and distribution of roots determines the location of root exudates, litter inputs and nutrient uptake.
	See traits associated to "Plant N acquisition"	Whole root system, absorptive roots	van der Krift & Berendse, 2001; Scherer-Lorenzen *et al.,* 2003; Personeni & Loiseau, 2005; Batterman *et al.,* 2013b; Leroux *et al.,* 2013; Moreau *et al.,* 2019	Most traits associated to "Plant N acquisition" can be important for this process. The capacity of plants to acquire N from soil, and compete with microorganisms, across a range of locations in the soil influences N cycling.
	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.,* 1997; Fan & Guo, 2010; McCormack *et al.,* 2015	Influences the input of litter (and N-containing compounds) into the soil.
	Root litter nutrient release rate*	Whole root system, fine-roots	Parton *et al.,* 2007	Determines the rate at which N is transferred from litter to soil.
	Root N concentration*	Whole root system, absorptive roots	Hobbie *et al.,* 2006; Parton *et al.,* 2007; Legay *et al.,* 2014; Cantarel *et al.,* 2015; Thion *et al.*, 2016	Root N is positively related to litter N release rate (lower N immobilization rate), N mineralisation and nitrification (e.g. archaeal ammonia oxidisers are more abundant in the rhizosphere of high N roots than low N roots).
	Mycorrhizal association type*	Absorptive roots	Phillips *et al.,* 2013; Lin *et al.,* 2017; Wurzburger & Brookshire, 2017; Zhu *et al.,* 2018	Ecosystems dominated by AM, ERM and ECM plants are characterized by different C and mineral nutrient cycles due to the different enzymatic capacities of the symbionts. AM, ECM, and ERM fungi represent a gradient from limited saprotrophic capabilities and greater reliance on inorganic N as primary N source to the ability to produce extracellular enzymes and greater use of increasingly complex organic N forms.
	Root exudation rate*	Fine-roots	Phillips *et al.,* 2011; Meier *et al.*, 2017; Moreau *et al.,* 2019	Enhanced root exudation increases soil microbial activity and accelerates the breakdown of (fast-cycling) organic N forms in the rhizosphere. Roots can exude/secrete nitrification and denitrification inhibitors.
Ecosystem P cycling				
	See traits associated to "Plant P acquisition"	Whole root system, absorptive roots	Lambers *et al.,* 2008; Ros *et al.,* 2018	Most traits associated to "Plant P acquisition", including traits associated to "Soil space occupancy", can be important for this process. The capacity of plants to acquire P from soil, with or without mycorrhizal symbiosis, across a range of locations in the soil influences P cycling.
	Root lifespan* and turnover*	Whole root system, fine-roots	Jackson *et al.,* 1997; Fan & Guo, 2010; McCormack *et al.,* 2015	Influences the input of litter (and P-containing compounds) into the soil.

	Root litter nutrient release rate*	Whole root system, fine-roots	Fujii & Takeda, 2010	Determines the rate at which P is transferred from litter to soil.
	Root P concentration*	Whole root system, fine-roots	Seastedt, 1988; McGrath *et al.,* 2000; Manzoni *et al.,* 2010	Can be a major driver of soil P availability in P-limited soils.
Soil water holding capacity				
	See traits associated to " Ecosystem C cycling"	Fine-roots	Rillig & Mummey, 2006; Poirier *et al.,* 2018	Root and mycorrhizal traits favouring C accumulation in soil and improving soil aggregate stability, improve soil water holding capacity.
	Root mass and length density* (+)	Fine-roots	Noguchi *et al.,* 1997	After death and decay, roots leave empty galleries and pores favourable to water retention. Roots also contribute to organic matter accumulation, which increases soil water holding capacity.
	Root turnover* (+)	Fine-roots	Noguchi *et al.,* 1997; Perillo *et al.*, 1999	After death and decay, roots leave empty galleries and pores favourable to water retention. Roots also contribute to organic matter accumulation, which increases soil water holding capacity.
	Mean root diameter*	First-order roots	Norton *et al.,* 2004; Ghestem *et al.,* 2011; Soto-Gomez *et al.,* 2018	Larger roots leave larger pores that, depending on the context, may be favourable or detrimental to water retention.
Bedrock weathering				
	Root exudation rate* (+)	Fine-roots	Ochs *et al.,* 1993; Hinsinger, 1998; Phillips *et al.,* 2009; He *et al.,* 2012; Houben & Sonnet, 2012	Exudation of organic acids and enzymes by roots enhance bedrock weathering. Additionally, C flux to the rhizosphere stimulates the weathering activity of root microbiome.
	Maximum rooting depth* (+)	Whole root system	Richter & Markewitz, 1995; Schwinning, 2010; Maeght et al., 2013	Deep-rooted species are most likely to reach bedrock.
	Root mass and length density* (+)		Hinsinger *et al.,* 1992	Increases root overall impact on bedrock.
	See traits associated to "Root penetration of soil" (+)	Whole root system	Bengough, 2012; Kolb *et al.,* 2012	Root growth pressures may help to extend cracks in weathering bedrock. Root elongation within a rock crack depends on the balance of axial and radial pressures.
	Mycorrhizal association type*	Fine-roots	Taylor *et al.,* 2009; Pawlik *et al.,* 2016	There is stronger evidence for bedrock weathering from ECM activity than this of AM.
	Mycorrhizal fungi identity*	Fine-roots	Jongmans *et al.,* 1997; Hoffland *et al.,* 2004; Schwinning, 2010.	Due to differences in rates of chemical exudation, hyphal production, and exploration distances among species of mycorrhizal fungi, species identity is likely to be an important determinant for faster or slower weathering rates.
	Root secondary growth (+)	Whole root system	Misra *et al.,* 1986; Richter & Markewitz, 1995	The radial force widening a crack is the product of the radial pressure and the contact area of root surface in the crack.
Hydraulic redistribution				
	Diverse root growth angles* (+)	Whole root system	Hultine *et al.,* 2003a; Hultine *et al.,* 2003b Scholz *et al.,* 2008; Siqueira *et al.,* 2008	Extensive distribution of roots in higher and lower soil horizons allows connection between wet and drier soil layers.

	Maximum rooting depth* (+)	Whole root system	Burgess *et al.,* 1998; Burgess, 2000; Scholz *et al.,* 2008; Maeght *et al.*, 2013	Presence of roots at depth allows access to wetter soil layers in soils experiencing drying of the upper horizons, which is critical for hydraulic lift.
	See traits associated to "Plant resistance and survival to drought" (+)	Whole root system, absorptive roots	Domec *et al.,* 2004; McElrone *et al.,* 2007; Warren *et al.,* 2008; Grigg *et al.,* 2010; Prieto *et al.,* 2012a ;Prieto *et al.,* 2014	Most traits favouring "Plant resistance to drought", including traits favouring "Plant water acquisition", will contribute to maintaining a functional root system during periods of soil drying and therefore allow hydraulic redistribution.
	See traits associated to "Plant water acquisition" (+)	Whole root system, absorptive roots	Egerton-Warburton *et al.*, 2008; Prieto *et al.*, 2012b	Root and mycorrhizal traits favouring "plant water acquisition" increase water flow through the root system.
	Vertical root mass distribution index* (+)	Whole root system	Schenk & Jackson, 2002a, 2002b	High proportion of roots in deeper soil horizons may reinforce hydraulic lift.
	Root turnover* (+)	Absorptive roots	Espeleta *et al.,* 2004	Determines the presence of active roots in soil layers that absorb and redistribute water.
	See traits associated to "Plant lateral spread and belowground dispersal" (+)	Whole root system	Jónsdóttir & Watson, 1997; Stuefer, 1998	Redistribution of water can occur in the horizontal plane via plant clonal connectors.
Ecosystem evapotranspiration				
	See traits associated to "Plant water acquisition" (+)	Whole root system, absorptive roots	Nepstad *et al.,* 1994; Augé *et al.,* 2008; Fort *et al.,* 2017	Most traits associated to "Plant water acquisition" facilitate the transfer of water from the soil to the plant and favour evapotranspiration.
	See traits associated to "Hydraulic redistribution" (+)		Domec *et al.*, 2010	Facilitates the transfer of water from deep soils to shallower soil horizons.
Soil inter-particle cohesion				This property relates to soil surficial erosion.
	See traits associated to "Soil space occupancy" (+)	Whole root system, fine-roots	Angers & Caron, 1998; Gould *et al.,* 2016; Poirier *et al.,* 2018	Most traits increasing "Soil space occupancy" contribute to stabilizing soil macroaggregates through entanglement of soil particles, production of exudates, binding and compressing soil particles, and root-induced wetting and drying cycles.
	Root exudation rate* (+)	Fine-roots	Carminati *et al.*, 2016; Baumert *et al.,* 2018; Poirier *et al.,* 2018	Exudates (especially polysaccharides and cations) act as binding agents to initiate microaggregate formation and stabilize macroaggregates. Exudates also clog aggregate pores and induce water repellency.
	Mycorrhizal colonisation intensity* (+)	Absorptive roots	Rillig *et al.,* 2015; Poirier *et al.,* 2018	Mycorrhizal fungi produce exopolymers and proteins that glue and bind soil particles. The release of hydrophobins by ECM increases aggregate hydrophobicity. In addition, hypha enmesh soil fine particles within micro and macro aggregates.
	Root hemicellulose content (+)	Whole root system	Poirier *et al.,* 2018	Hemicellulose contains pentoses and uronics acids that stabilize soil aggregates.
	Root suberin content (+)	Whole root system	Bachman *et al.,* 2008; Poirier *et al.,* 2018	Suberin increases aggregate hydrophobicity and soil water repellency.
	See traits associated to "Plant water acquisition" (+)	Whole root system, absorptive roots	Czarnes *et al.,* 2000	Soil inter-particle cohesion is affected by wetting-drying cycles that increase the strength of organic binding agents.
Soil reinforcement against shallow landslides				

	Maximum rooting depth* (+)	Whole root system	van Beek *et al.,* 2005	Deep growing roots are more likely to cross the potential soil shear surface (zone within the soil where failure initiates), which enhances soil reinforcement.
	Vertical root length distribution index* (+)	Whole root system	Ghestem *et al.,* 2014	A greater number of branched roots below the shear plane will enhance root anchorage and so improve soil shear resistance.
	Root area ratio (+)	Whole root system	Wu, 1976; Bischetti *et al*., 2005; Mao *et al*., 2012	The greater the root area ratio of coarse and fine-roots (although roots > 2 cm in diameter contribute less) crossing the potential failure zone, the more the soil shear strength is increased, thus improving soil reinforcement.
	Root length density* (+)	Whole root system	Ennos, 1993; Stokes *et al.,* 2009	Increasing root length augments the pull-out resistance up to a critical length, from which roots will break in tension instead of slipping out of the soil.
	Root branching angle* (+)	Tap and sinker roots	Ghestem *et al.,* 2014	Vertically oriented roots increase soil shear resistance.
	Tensile strength* (+)	Whole root system	Chimungu *et al.,* 2015; Giadrossich *et al.,* 2017, 2019; Mao *et al.,* 2018	A higher tensile strength will enable a root to mobilise its full strength as it is pulled out of soil, thereby increasing soil shear strength.
	Modulus of elasticity* (+)	Whole root system	Cohen *et al.,* 2009; Mao *et al.,* 2018	Roots with large elastic modulus can remain anchored in soil, even after soil failure has occurred, thus holding vegetation in place and retarding or preventing mass substrate failure.
	Root bending resistance (+)	Tap, sinker and lateral roots	Goodman *et al.*, 2001	During landslide, thick structural roots act like soil nails that bend, preventing soil collapse, before breaking.
	See traits associated to "Plant water acquisition"	Whole root system, absorptive roots	Boldrin *et al.,* 2017	Rapid water acquisition will maintain soil in a drier state that offers greater resistance to deformation.

CC: colour code, in dark blue: trait of prime importance for performing the ecosystem process or property in at least some environmental conditions; medium blue: trait of secondary importance in at least some environmental conditions; light blue: trait of potential but unknown importance due to missing or low experimental evidence. * refers to traits whose measurement protocols are described in Freschet *et al.* (2020). (+) versus (-) refers to the positive or negative effect of one trait on the function, respectively. 'Entity of interest' refers to a range of plant belowground parts as described in Freschet *et al.* (2020). The full list of references is available as Supplementary Notes S1.

Table 3. Overview of studies testing the relationships between root traits and plant N uptake capacity.

Reference	Function measured	Units	Method used	Temporal scale	Spatial scale	Root or plant traits measured (and relationship found)	Root entities	Number of species	Growth forms	Biome
Bowsher *et al.,* 2016	Short-term net uptake rate	µmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	30 h	Pot	Specific root length (ns), root tissue density (ns)	Whole root system	6	Forbs (6)	
Craine *et al.,* 2003	Long-term net uptake rate	mg N kg^{-1}	Soil NH_4^+ and NO_3^- sampling		Pot	Fine root mass density (+), coarse root mass density (ns)	Fine roots (<2mm)	11	Graminoids (6), forbs (3), Legumes (2)	Temperate
de Vries & Bardgett, 2016	Long-term net uptake rate	kg N ha^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	48 h	Pot	Root biomass (+), specific root length (ns), root tissue density (-), root N concentration (ns)	Whole root system	24	Graminoids (12), forbs (12)	Temperate
Dybzinski *et al.,* 2019	Long-term net uptake rate	g N m^{-2} day^{-1}	Whole plant N increment	95-110 days	Pot	Fine root mass (ns in 62% of cases; linear + in 5% of cases; saturated in 33% of cases)	Fine roots (<1mm)	18	Graminoids (5), Forbs (2) Tree (11)	
Dybzinski *et al.,* 2019	Long-term net uptake rate	g N m^{-2} day^{-1}	Whole plant N increment		Field	Fine root mass (ns: 5 studies; linear +: 2 studies)	Fine roots (<1mm)	7	Tree (7)	
Ficken & Wright, 2019	Long-term net uptake rate	mg N g^{-1} leaf	^{15}N tracers of NH_4^+ and NO_3^-	10 days	Pot	Root tip number per biomass (+), fine:coarse root volume (+), leaf nitrogen content (+)	Whole root system	4	Shrub (3), Tree (1)	Temperate
Freschet *et al.,* 2018	Short-term net uptake rate	µg N m^{-1} root h^{-1} and µg N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	6 h	Pot	Root mass fraction (ns), deep root fraction (ns), specific root length (ns), root hair length (ns), root interbranch distance (ns), root N concentration (ns), leaf mass fraction (ns), specific leaf area (ns), maximum leaf photosynthetic capacity (ns), plant height (-)	Absorptive roots	9	Graminoids (3), forbs (3), Legumes (3)	Temperate
Garnier *et al.,* 1989	Long-term net uptake rate	mg N g^{-1} root day^{-1}	Whole plant N increment	28 days	Hydro-ponics	Relative growth rate (+)	Whole root system	14	Graminoids (4), forbs (10)	Temperate
Garnier *et al.,* 1989	Short-term net uptake rate	mg N g $root^{-1}$ day^{-1}	NO_3^- depletion in nutrient solution	90 min	Hydro-ponics	Relative growth rate (+)	Whole root system	7	Graminoids (2), forbs (5)	Temperate
Garnier, 1991	Long-term net uptake rate	mg N g $root^{-1}$ day^{-1}	Whole plant N increment	17-28 days	Hydro-ponics	Relative growth rate (+)	Whole root system	21	Graminoids (9), forbs (12)	Temperate

Grassein *et al.,* 2015	Imax, Km	µmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+	5 min	Common garden	Imax NH_4^+: Specific root length (ns), root dry matter content (ns), root N concentration (+), specific leaf area (+), leaf dry matter content (ns), shoot N content (ns), shoot:root ratio (+) Km NH_4^+: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (ns), leaf dry matter content (+), shoot N content (ns), shoot:root ratio (ns)	Whole root system	8	Graminoids (8)	Temperate
Grassein *et al.,* 2015	Imax, Km	µmol N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	5 min	Common garden	Imax NO_3^-: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (+), leaf dry matter content (ns), shoot N concentration (ns), shoot:root ratio (ns) Km NO_3^-: Specific root length (ns), root dry matter content (ns), root N concentration (ns), specific leaf area (-), leaf dry matter content (+), shoot N concentration (ns), shoot:root ratio (ns)	Whole root system	8	Graminoids (8)	Temperate grassland
Grassein *et al.,* 2018	Imax	nmol N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+	1 h	Field + excised roots	Specific root length (ns), root dry matter content (-), root N concentration (+), specific leaf area (ns), leaf dry matter content (ns), leaf N content (+)	Absorptive roots	3	Graminoids (3)	Temperate
Grassein *et al.,* 2018	Imax	nmol N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	1 h	Field + excised roots	Specific root length (+), root dry matter content (-), root nitrogen concentration (+), specific leaf area (ns), leaf dry matter content (ns), leaf N content (+)	Absorptive roots	3	Graminoids (3)	Temperate grassland
Hodge, 2003	Long-term net uptake rate	mg N (^{14}N+^{15}N)	^{15}N tracers of labelled ^{15}N shoot material	22 days	Pot	In mixtures: Root length (+), mycorrhizal inoculation (+) In monocultures: Root length (ns), mycorrhizal inoculation (ns)	Whole root system	2	Graminoids (1), forbs (1)	Temperate
Hodge *et al.,* 1998	Long-term net uptake rate	µg N	^{15}N tracers of labelled organic material in patches	39 days	Pot	Root biomass (ns), root length (ns)	Whole root system	5	Graminoids (5)	Temperate
Hodge *et al.,* 1999	Long-term net uptake rate	µg N	^{15}N tracers of labelled organic material in patches	56 days	Pot	Root length density (+)	Whole root system	2	Graminoids (2)	Temperate grasslands
Hong *et al.,* 2018	Short-term net uptake rate	µg N m^{-1} root h^{-1}	^{15}N tracers of NH_4^+ or NO_3^- or Glycine or (NH_4^+ + NO_3^- + Glycine)	24 h	Field	Root surface area (+), specific root length (+), root diameter (-), root biomass (-)	Whole root system	10	Graminoids (3), forbs (4), legumes (3)	Alpine grassland

Kulmatiski *et al.,* 2017	Short-term net uptake rate	% cm^{-1} root	^{15}N tracers of NH_4^+ and NO_3^-	72 h	Field	Root biomass (ns)	Whole root system (absorptive)	5	Graminoids (3), forbs (1), Shrub (1)	
Larson & Funk, 2016	Long-term net uptake rate	µg N day^{-1}	Whole plant N increment	28-58 days	Pot	Root growth rate (+), root elongation rate (+), root mass fraction (-), specific root length (+), root diameter (-)	Whole root system (absorptive)	18	Graminoids (4), forbs (7), Trees (7)	Temperate
Leffler *et al.,* 2013	Short-term net uptake rate	µg N g^{-1} root h^{-1}	^{15}N tracers of NO_3^-	2 h	Pot	Root mass (+), root length (+), specific root length (+)	Whole root system	5	Graminoids (5)	Temperate
Levang-Brilz & Biondini, 2003	Long-term net uptake rate	g N m^{-2} root day^{-1}	Whole plant N increment	60-90 days	Pot	Root:shoot ratio (+), relative growth rate (saturated relationship)	Whole root system	55	Graminoids (17), forbs (29), legumes (7), shrubs (2)	Temperate
Liu & Kleunen, 2019	Long-term net uptake rate	g N g^{-1} root day^{-1}	Whole plant N increment	26 days	Pot	Root mass fraction (-)	Whole root system (absorptive)	41	Graminoids (11), forbs (26), Legumes (4)	Temperate
Ma *et al.,* 2018	Short-term net uptake rate	µg N g^{-1} root h^{-1}	^{15}N tracers of NH_4^+ and NO_3^-	90 min	Field	Specific root length (ns), root diameter (ns)		17	Trees (17)	Grassland, boreal, temperate, subtropical, tropical
Ma *et al.,* 2018	Long-term net uptake rate	µg N g^{-1} root h^{-1}	Whole plant N increment	7 days	Field	Specific root length (ns), root diameter (ns)		17	Trees (17)	Grassland, boreal, temperate, subtropical, tropical
Maire *et al.,* 2009	Imax, Km	mg N g^{-1} root h^{-1}	NH_4^+ and NO_3^- depletion in nutrient solution	90 min	Common garden	Imax: Root dry mass (ns), root area (-), leaf N concentration (+)	Absorptive roots	13	Graminoids (13)	Temperate
Maire *et al.,* 2009	Long-term net uptake rate	g N m^{-3} y^{-1}	Shoot plant N increment	209-212 days	Common garden	Root dry mass (+), leaf N concentration (ns)	Absorptive roots	13	Graminoids (13)	Temperate
Osone *et al.,* 2008	Long-term net uptake rate	g N g^{-1} root day^{-1}	Whole plant N increment		Pot	Relative growth rate (+), root:shoot ratio (-), specific leaf area (+), leaf N concentration per area (-), net assimilation rate (+)	Whole root system (absorptive)	11	Forbs (6), Trees (5)	
Poorter *et al.,* 1991	Long-term net uptake rate	nmol N g $root^{-1}$ day^{-1}	Whole plant N increment	17 days	Hydro-ponics	Relative growth rate (+)	Whole root system	24	Graminoids (11), forbs (13)	Temperate

Ravenek *et al.,* 2016	Short-term net uptake rate	µmol N m^{-1} root h^{-1}	Li and Rb uptake rate (surrogate tracers)	46 h	Pot	Relative growth rate (ns), selective root placement (ns), root length density (ns), specific root length (ns)	Absorptive roots	8	Graminoids (4), forbs (4)	Temperate
Reich *et al.,* 1998	Long-term net uptake rate	mg N g^{-1} root day^{-1}	Whole plant N increment	61 days	Pot	Specific root length (+), root length ratio (+), root respiration (+), relative growth rate (+)	Whole root system	9	Trees (9)	Boreal forest
Robinson *et al.,* 1991	Long-term net uptake rate		Whole plant N increment	97 days	Pot	Root length density (ns)	Whole root system (absorptive)	1 (13 karyo-types)	Graminoids (1)	Temperate
Wiesler & Horst, 1994	Long-term net uptake rate	kg N ha^{-1}	Soil NO_3^- depletion and shoot uptake rate		Field	Root length density (+)	Whole root system	1 (10 maize cultivars)	Graminoids (1: crop)	Temperate
Zerihun & Bassirirad, 2001	Imax, Km	µmol N g^{-1} root h^{-1}	NO_3^- and NH_4^+ depletion	12 h	Pot	Imax NH_4^+: Relative growth rate (+), biomass allocation (ns) Km NH_4^+: Relative growth rate (+)	Fine (<1mm) & coarse roots	6	Trees (6)	Temperate

The full list of references is available as Supplementary Notes S1.

Table 4. Overview of studies testing the relationships between root traits and soil reinforcement against shallow landslides.

References	Property measured	Method used	Soil type	Soil moisture content	Root or plant traits measured (and relationship found)	Root entities	Number of species	Growth forms	Biomes
Docker & Hubble, 2008	Increase in shear stress in soil matrix due to roots (kPa)	In-situ testing with a large shear box (ranged from 0.4 x 0.4 to 0.5 x 0.5 at the base and 0.21 - 0.44 m in height)	Brown loam and sandy loam	Saturated	Root area ratio of roots crossing the shear plane (+)	Whole root system	4	Trees (4)	Subtropical rainforest, subtropical dry forest
Fan & Chen, 2010	Soil matrix shear strength (kPa)	In-situ testing with a large shear box (0.3 x 0.3 x 0.2 m)	Clayey and sandy soils	12-14%	Cumulated tensile strength of all roots per unit area of soil (+), cumulated tensile strength of all roots crossing the shear plane (+)	Roots < 20 mm	5	Trees (5)	Tropical rainforest
Ghestem *et al.*, 2014; Veylon *et al.*, 2015	Tangential shear stress at yield point (kPa) of soil matrix	Laboratory testing with a large shear box (0.5 x 0.5 x 0.3 m)	Alluvial silty clay	9-21%	Roots crossing the shear plane: cross-sectional area of coarse roots (+), number of coarse roots (+), fine root mass (+), number of coarse root branches per unit length (ns), coarse root length (ns), coarse root diameter, coarse root volume (ns), fine root mass density (ns) Roots above the shear plane**: c**oarse root length (+), number of coarse root branches per unit length (+), number of coarse roots (ns), cross-sectional area of coarse roots (ns), diameter of coarse roots (ns), coarse root volume (ns), fine root mass (ns), fine root mass density (ns) Roots below the shear plane: number of coarse root branches per unit length (+), coarse root volume (+), fine root mass (+), number of coarse roots (ns), cross-sectional area of coarse roots (ns), coarse root diameter (ns), coarse root length (ns), fine root mass density (ns).	Whole root system	3	Trees (3)	Subtropical rainforest
Normaniza *et al.*, 2008; Ali & Osman, 2008	Soil matrix shear strength (kPa)	Laboratory testing with a large shear box (0.3 x 0.3 x 0.2 m)	Silty sand	Not known	Root length density (+), root diameter (+)	Whole root system	3	Trees (2), Shrubs (1)	Tropical rainforest
Wu *et al.*, 1988	Force applied to shear soil matrix (N)	In-situ testing with a large shear box (0.6 x 0.3 x 0.3 m)	Sandy silt, gravelly silt, silty clay and sand	Partially saturated	Cumulated tensile force of all roots crossing the shear plane (+ in sandy and gravelly silt soils only, 2 species). Cumulated tensile force of all roots crossing the shear plane (ns in silty clay, 1 species).	Whole root system	3	Trees (3)	Boreal forest, temperate forest

The full list of references is available as Supplementary Notes S1.

Figure captions

Figure 1. Plant and ecosystem functioning typically relate to a wide range of root traits (a, b, c) from a wide range of fields of root ecology (d). Meanwhile, some traits play multiple roles in a range of functions, as illustrated by a subset of functions associated to (a) resource acquisition and (b) resource protection and use by plants, and the (c) cycling of elements in ecosystems; as well as a (d) compilation of the relative occurrence of traits from several sub-disciplines of root ecology in these three examples. Traits with an * refer to traits whose measurement protocols are described in Freschet *et al.* (2020). Traits connected to at least two functions are shown in bold font and those highly represented across all three panels (a, b and c) are further highlighted in green font. Colours of lines and text boxes are only for visual effects.

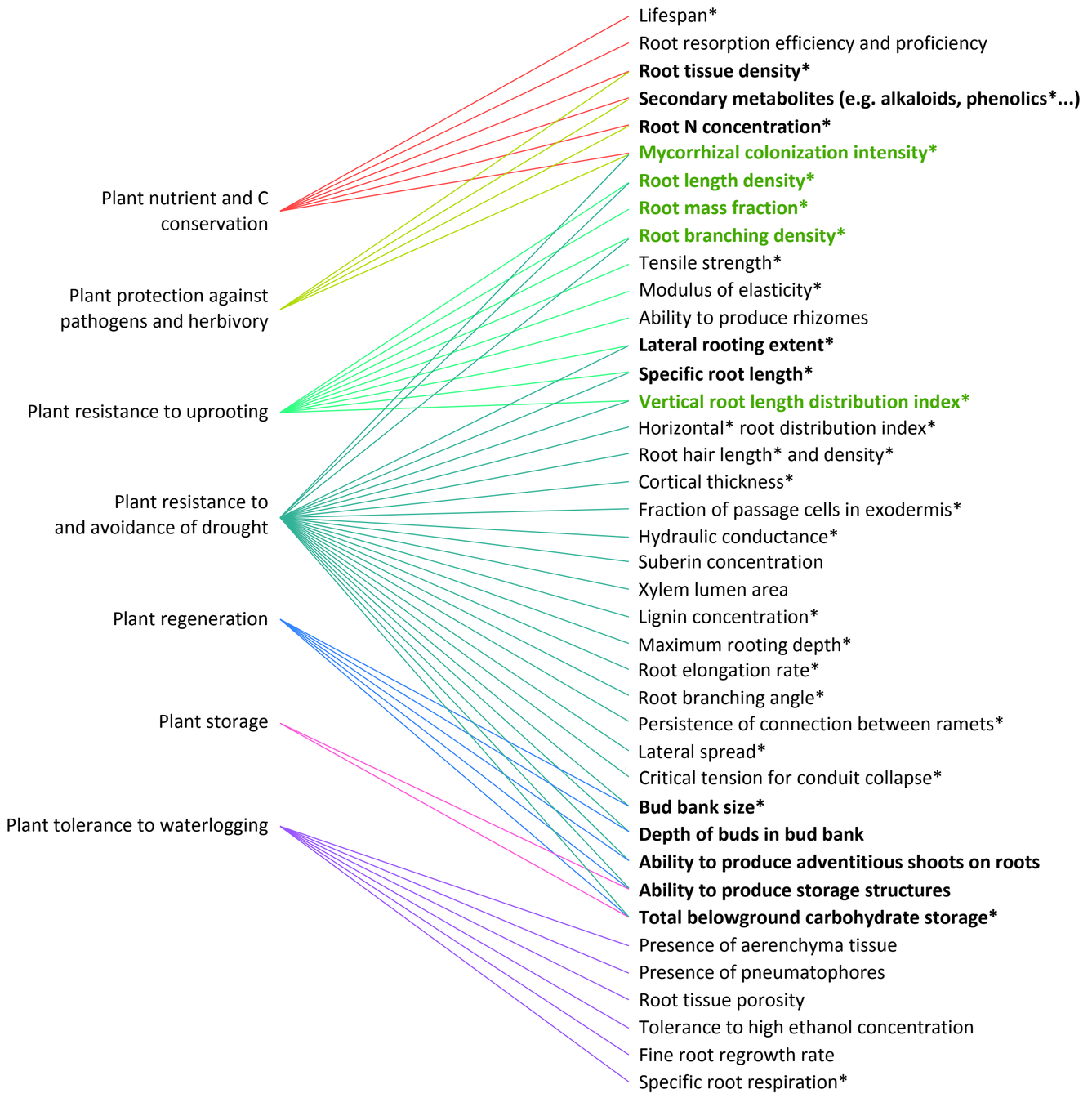
Figure 2. Direct, indirect and hierarchical relationships between the (non-exhaustive) range of root traits that have been linked to (a) long- and short-term N uptake and (b) soil reinforcement against shallow landslides. Black arrows represent causal relationships. + and - represent the direction of the relationship. Trait position along the vertical axis depicts trait hierarchical relationships, with lower levels representing 'composite' traits and upper levels representing 'underlying' traits (see main text). Major trait covariations are also shown with orange dotted arrows. The ease of trait measurement is approximated by colour ranging from blue ('hard' traits) to green ('soft' traits). * 'Enzymes' refers to the range of enzymes related to N uptake, assimilation and transport in roots. Imax stands for ‘root maximum net ion uptake rate’ and Km for ‘root Michaelis-Menten constant’.

Supporting Information

Notes S1. Full list of references for papers cited in Tables 1, 2, 3 and 4.

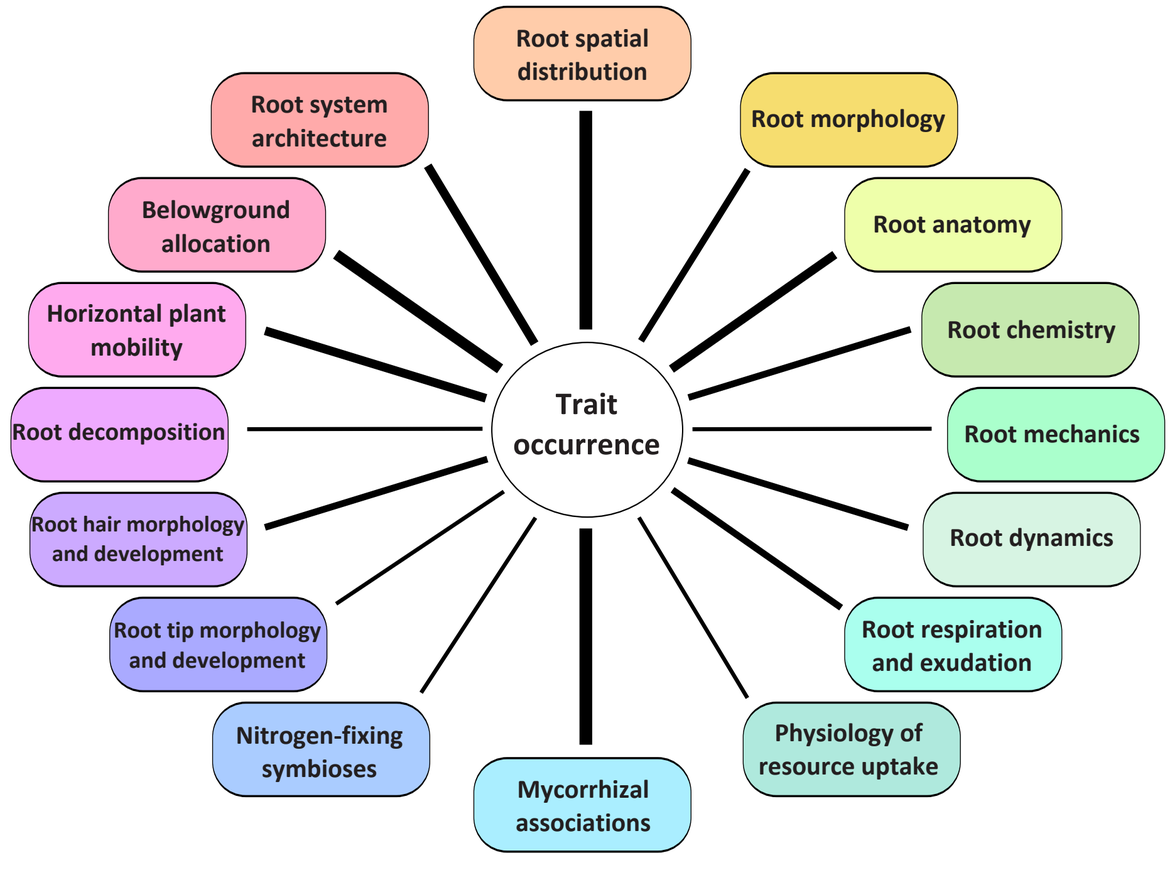
(a) Resource acquisition

(b) Resource protection and reuse

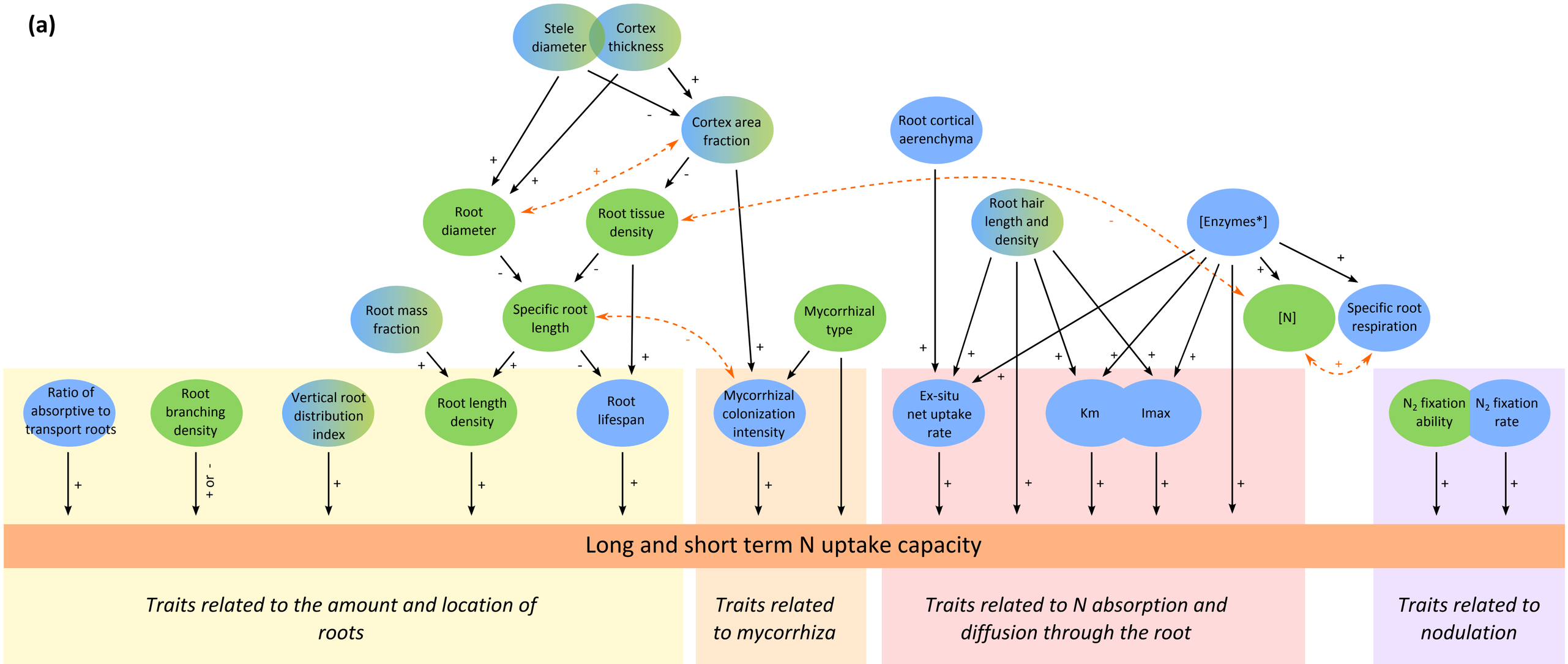


(c) Cycling of elements

(d) Representation of different fields of root ecology (as presented in Freschet *et al.*, 2020) across this subset of 14 plant and ecosystem functions. The thicker the line the higher the trait occurrence.

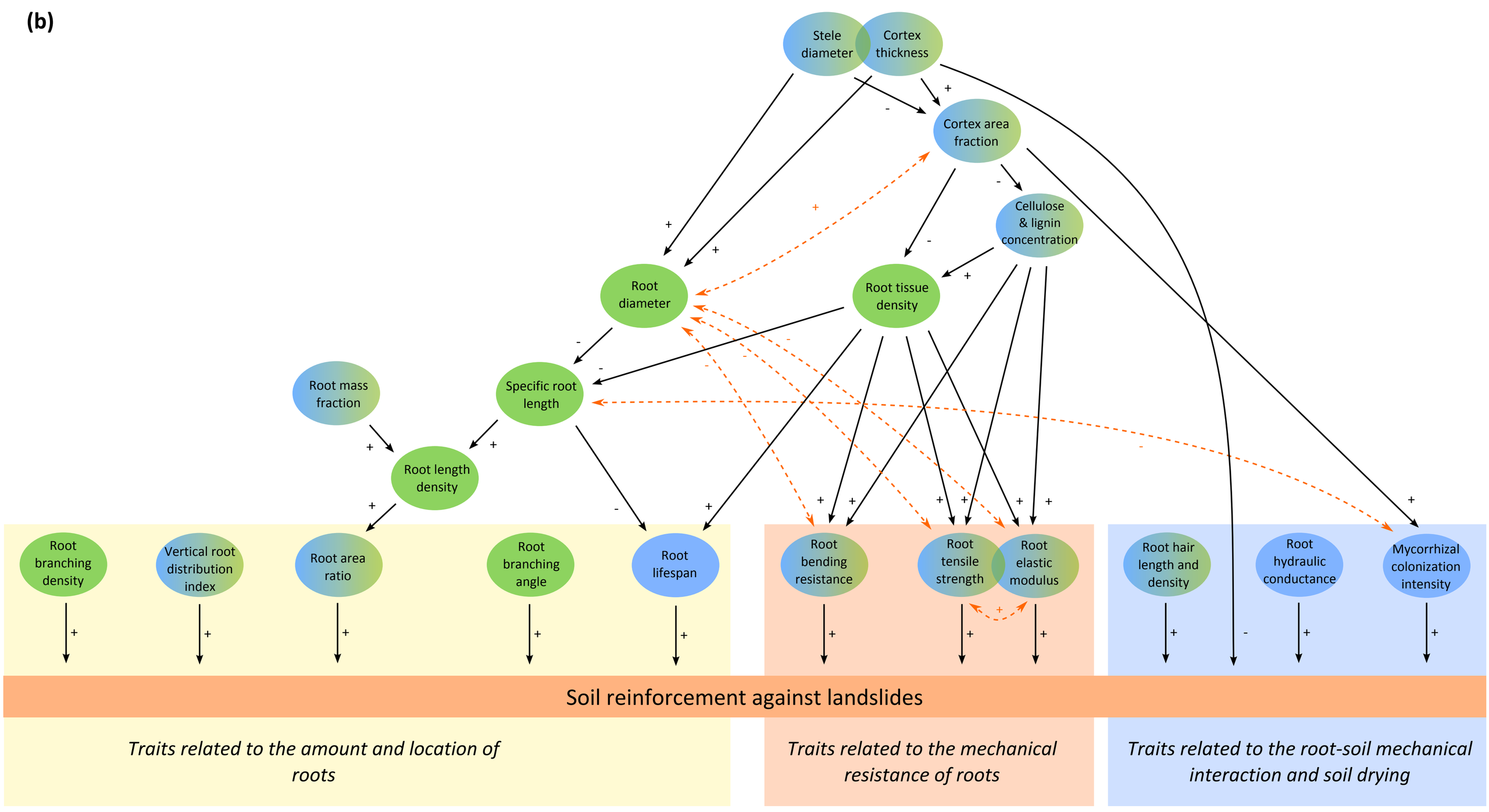


(a)



Uptake capacity is greatest when the soil volume is efficiently explored and/or exploited, and when the root is metabolically active towards N absorption or promote active resource exchange via symbiotic associations.

(b)



Reinforcement is greatest when a number of roots cross a potential shear plane, when the root tissue is mechanically strong and with a large elastic modulus, and when roots are strongly bonded to the soil and dry the soil rapidly.